FORAGING BEHAVIOR OF JUVENILE STELLER SEA LIONS

IN THE GULF OF ALASKA

A Thesis

by

WENDY JANE SCHRADER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2006

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Co-Chairs of Committee,	Markus Horning
	Bernd Würsig
Committee Members,	Fran Gelwick
	Doug Biggs
Head of Department,	Robert Brown

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ABSTRACT

Foraging Behavior of Juvenile Steller Sea Lions

in the Gulf of Alaska. (May 2006)

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Dr. Bernd Würsig

Relating the behavior of predators to prey density is an important aspect of foraging theory. Changes in prey accessibility may have contributed to a greater-than 80% decline in Steller sea lions (*Eumetopias jubatus*) throughout the western portion of their range during the last 30 years. A new method was developed for inferring prey accessibility to juveniles of this otariid, from observable features of diving and ranging behavior. Seventeen juveniles (9F, 8M) were monitored in multiple seasons and locations in the Gulf of Alaska via satellite telemetry. Twelve of the 17 had experienced 1-3 months of temporary captivity. Effects of temporary captivity on endurance, habitat use and development of diving and ranging behavior were tested. Diving and ranging patterns of previously captive juveniles were consistent with data reported for free-ranging juveniles. Development in mean dive depth and duration after release was likely due to increased foraging. "Focus in time spent at depth" was tested as a proxy for prey accessibility using predictions based on foraging theory. 'Focus…' was defined as vertical concentration in dive distribution and was calculated by comparing the observed time spent at depth with an expected distribution. There was significantly more focus in

summer than winter, and more focus at depth (>62 m) in winter. Focus at depth was significantly greater during midday for juveniles monitored in winter. Significant negative correlation between maximum focus and trip duration provided the best indication that focus may be related to prey accessibility. Short trips had significantly greater maximum focus than long trips, using a matched-pairs approach. Analysis of focus in time-at-depth data can elucidate small scale interactions between juvenile otariids and their prey. This new method of measuring the dive behavior of otariids can be applied to individual foraging trips and holds promise as a proxy for assessing seasonal, annual and developmental changes in individual prey accessibility.

DEDICATION

This thesis is dedicated to my Grandfather

Milton Oliver Peach

ACKNOWLEDGEMENTS

This work would not have been possible without the assistance and encouragement of my thesis advisor, Markus Horning. Thank you for your constant support and inspiration. Jo-Ann Mellish and the Alaska SeaLife Center also provided logistical support, materials, workspace and all of the many tools necessary to accomplish the work. I am deeply indebted to them for their support throughout my thesis work. I thank the amazing animal husbandry staff at the Alaska SeaLife Center including Dennis Christen, Elizabeth Moundalexis and many others for their ingenuity and persistence.

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Thank you, Timothy Michael Markowitz; “There but for the grace of you go I” Thank you to my amazing family for your creativity and determination, and for teaching me how to win in life. Thank you, Mom, for your brilliant mind. Thank you, Dan, for your strength and courage. Thank you, John, for your love of life. Thank you to my sister in faith, Maggie Rose Eisenberg. Next time we’ll go first class. Last but not least, thank you T. Schrader and “Max” for your late night support.

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CHAPTER I

INTRODUCTION

The largest extant member of the Family Otariidae, the Steller sea lion (*Eumetopias jubatus*), reproduces and develops at high latitudes, experiencing high seasonal fluctuation in temperature, sea-surface conditions and prey availability common to sub-arctic climates. Changing demographics of breeding populations indicate that reduced juvenile survival may have caused a significant decline in Steller sea lion abundance beginning in the 1970's (York 1994; DeMaster et al. 2001a). Although initial abundance estimates were relatively high (>250,000), the current population estimate for Steller sea lions in the United States is approximately 84,000 with about 39,000 making up the western portion of the population (Angliss and Lodge 2003). This decline in abundance, particularly for the western portion of the population, has been attributed to nutritional stress (Alverson 1992; Alaska Sea Grant 1993; Merrick et al. 1997; Calkins et al. 1998).

The seasonal variation in foraging habitat experienced by the Steller sea lion makes this species a good candidate for an examination of the behavioral response of a diving predator to changes in prey accessibility. Changes in prey density in time and space may influence the degree of vertical focus exhibited by diving predators. Vertical focus is a measure of variation in vertical distribution of time spent at depth during foraging dives. This study examines vertical focus in water-column use by juvenile Steller sea lions at various spatial and temporal scales, and tests this behavioral measure as an indicator of changes in individual prey accessibility.

This thesis follows the style and format of Behavioral Ecology and Sociobiology.

Definition of focus

For the purposes of this study, 'focus' is defined as the vertical concentration in space of a predator's diving behavior. More explicitly, focus is determined by:

1. Defining an expected distribution of time spent at depth for juvenile sea lions if their behavior is NOT focused and;

2. Comparing the observed time spent at depth with the expected distribution to assess where in the water column and to what extent diving is focused.

The expected distribution of time spent at depth if juvenile sea lions are not focused was determined by building a model of diving behavior that includes the typical behavior of juvenile Steller sea lions as reported in other studies, the method of data collection (i.e., binned data), and travel time to and from the surface. Details of this model are reported in the methods section of Chapter III. Throughout this thesis, the term 'focus' is used to describe differences in observed from expected time-at-depth (TAD) either between individuals or between individuals' foraging trips. A juvenile (or foraging trip) is considered to show greater focus to the extent that its behavior differs from the model.

Juvenile sea lions that exhibit greater focus are expected to have greater prey accessibility due to reduced search time when foraging. This expected difference in prey accessibility can be assessed either between individuals or between individuals' foraging trips. 'Prey accessibility' is defined as the availability and procurability of a prey item or prey patch to a predator based on the morphology, physiology, behavior and ecology of both predator and prey. This definition is derived from the definition for 'habitat

availability' as described in Hall et al. (1997) and takes into account not only the abundance of prey but also the procurability of prey to the predator. The reliability of the use of focus to assess changes in prey accessibility can be tested using other behavioral measures which are known to relate to prey accessibility for sea lions (e.g. foraging trip duration) or seasonal fluctuation in prey accessibility. Particular hypotheses relating to focus, other behavioral measures, and prey accessibility are outlined in detail in the methods section of Chapter III.

Steller sea lion biology

Steller sea lion rookeries and haul-outs may consist of fewer than five to hundreds of sea lions depending on season and time of day. Steller sea lions exhibit a high degree of sexual size dimorphism, with males up to four times larger than females. Adult males can reach 4 m in length and 1100 kg in mass, although average sizes for adult males are 2.7 m and 680 kg. Adult females average 2.1 m in length and 270 kg in mass. Steller sea lions are light brown to dark brown in color, with rounded snouts (Fig. 1). At birth, Steller sea lion pups average 1 m in length and 21 kg in mass (Fiscus 1961; Mathisen et al. 1962; Loughlin 1998; Winship et al. 2001; Fig. 1).

Both male and female Steller sea lions reach sexual maturity between 3 and 7 years of age, although adult males do not often hold a breeding territory before the age of 9 years. Females can breed into their twenties while adult males do not hold breeding territories after approximately 14 years of age. Females have one pup per year and nurse

pups for approximately 12 months, although two-year-old and even four-year-old-Steller sea lions have been known to nurse (Mamaev and Burkanov 2004).

Fig. 1 Variation in size for pup, juvenile and adult Steller sea lions is shown. TJ001, a male Steller sea lion from this study, is located in the center of the picture with an attached tag evident. Photo taken by J..N. Waite, Sept. 2003. Permit #881-1668-02.

The Steller sea lion has a polygynous mating system with breeding age males beginning to establish territories on known rookeries in late April/early May. By late May, females arrive at rookery sites to give birth to a single pup. Nursing and foraging activities of females follow the typical otariid pattern of a first trip to sea during the first 8-14 days after parturition, and foraging trips continuing throughout the summer (Gentry 1970; Calkins and Pitcher 1982; Gentry and Kooyman 1986). By late August, pups begin to enter the water and leave on foraging trips with females, often transiting to winter haul-

out locations for females and juveniles (Raum-Suryan et al. 2004), with some pups traveling over 120 km at ages as young as two months.

Steller sea lions range throughout the North Pacific Ocean, from the Channel Islands in Southern California to the Bering Sea and west to the Kuril Islands and Okhotsk Sea (Fig. 2). Although Steller sea lion haul-outs and rookeries are distributed

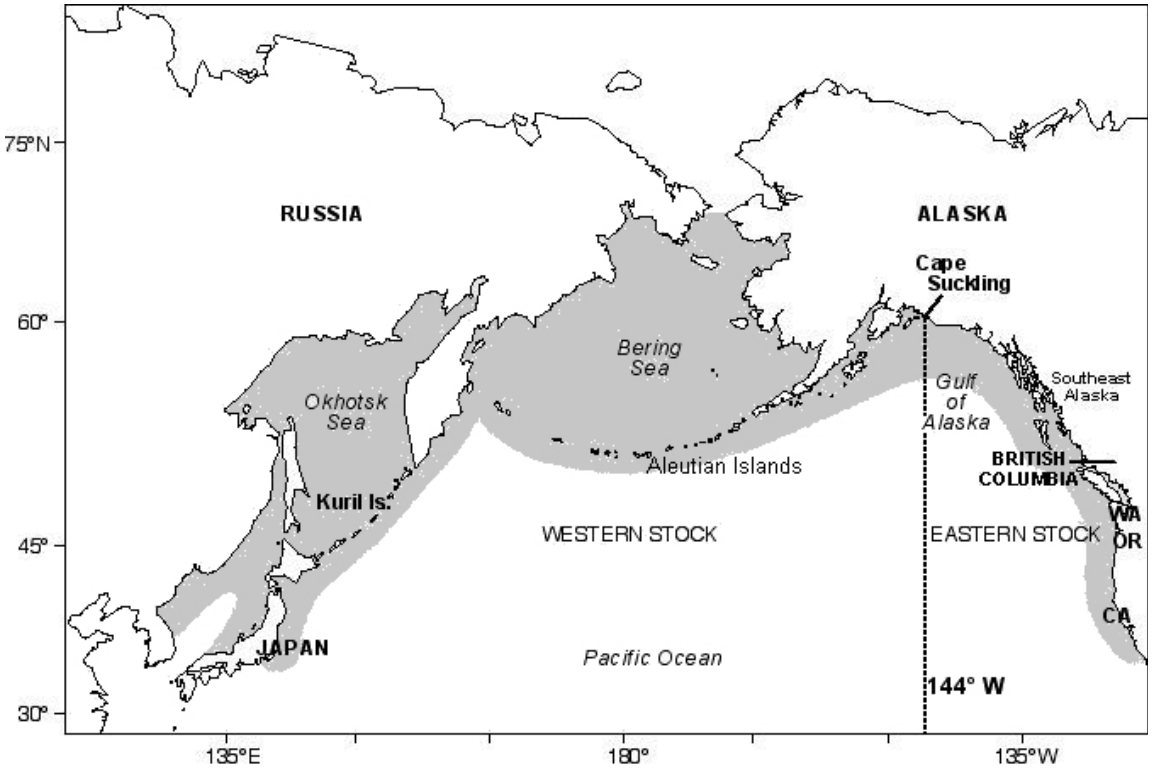


Fig. 2 The range of the eastern and western populations of Steller sea lions (NOAA National Marine Mammal Laboratory, Alaska Fisheries Science Center: http://nmml.afsc.noaa.gov)

widely throughout the North Pacific, population concentrations have historically occurred in the Aleutian Islands and the Gulf of Alaska (Calkins and Pitcher 1982). Established rookeries and haul-outs for Steller sea lions have been censused in these areas from as early as the 1950's, although regular censusing did not begin until the 1970's. Steller sea

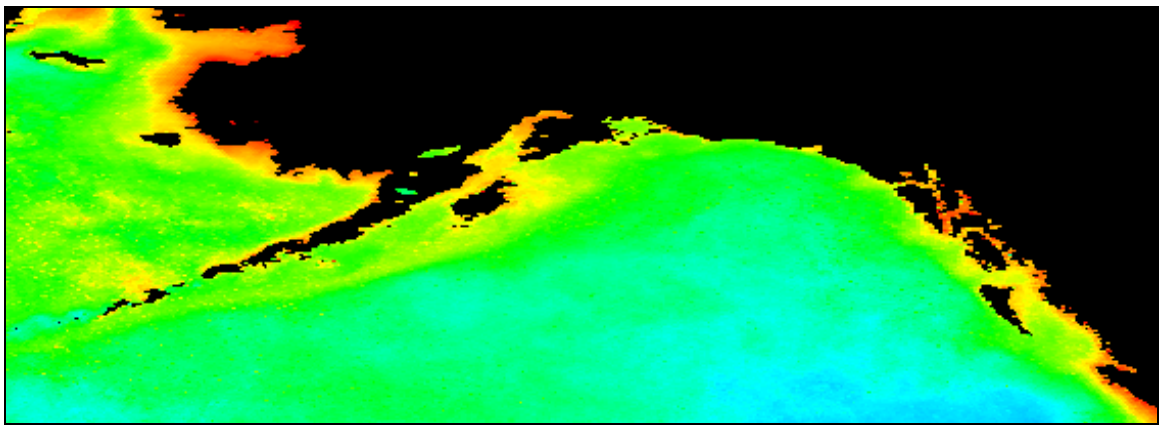
lions in the U.S. are divided into two distinct populations, based on mitochondrial DNA analysis, distributional data, and population response data (Bickham et al. 1996; York et al. 1996). The eastern and western U.S. Steller sea lion stocks, located east and west of 144°W (Cape Suckling, AK; Fig. 2), are managed separately. Steller sea lion rookeries and haul-outs in the Gulf of Alaska and Aleutian Islands are generally located in inaccessible areas on islands or remote coastlines.

Steller sea lions exhibit high breeding site fidelity (Calkins and Pitcher 1982; Merrick et al. 1994). Steller sea lion haul-outs and rookeries in Alaska are often adjacent to coastal waters >200 m deep, with high variation in bathymetry. Prey diversity is high, including such species as Pacific cod (*Gadus macrocephalus*), Pacific herring (*Clupea pallasi*), Pacific salmon (*Oncorhyncus*), Capelin (*Mallotus villosus*) and Arrowtooth flounder (*Atheresthes stomias*). Walleye pollock (*Theragra chalcogramma*) makes up a substantial proportion of Steller sea lion diet (Pitcher 1981; Frost and Lowry 1986; Springer 1992; Merrick et al. 1997; Calkins 1998; Sinclair and Zeppelin 2002). Based on data collected in the 1950's, Steller sea lions of the western stock had a high proportion of herring and other small, schooling fatty fishes in their diet (National Marine Fisheries Service 1992). Since the 1970's, gadid species, specifically walleye pollock, make up most of the diet of the western U.S. Steller sea lion population (Merrick et al. 1997).

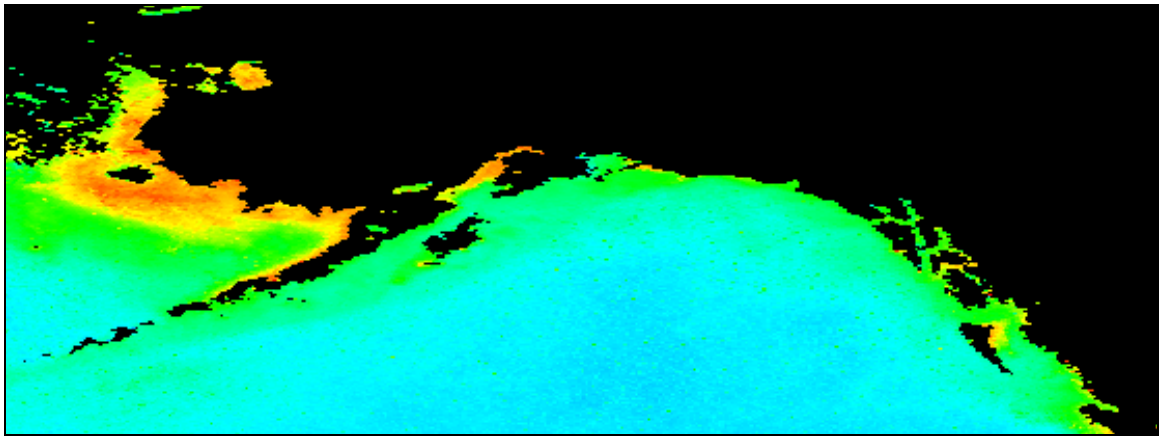
The habitat of the Steller sea lion in Alaska undergoes dramatic seasonal variation. Sea surface temperatures in the Gulf of Alaska range from 0ºC in February to 10-15ºC in August. The waters of the Gulf of Alaska are influenced by the Alaska Gyre, a divergent gyre which may create vertical movement of water from below the

thermocline of about 10 m/yr. This gyre is not as productive as it would be in lower latitudes due to light limitation in winter months (Lalli and Parsons 2001). Most primary

A. Summer



B. Winter



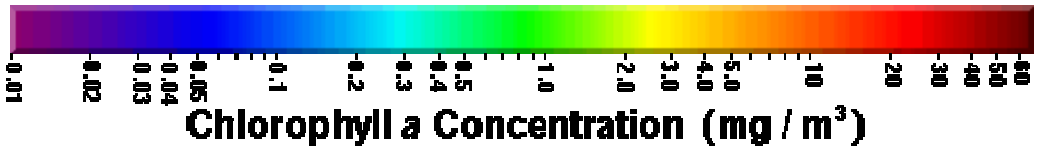


Fig. 3 **a** Summer and **b** winter chlorophyll *a* concentrations (scaled by color) in the Gulf of Alaska are compared. Composite SeaWiFS satellite data from 1998-2005 were used to build these figures (http://oceancolor.gsfc.nasa.gov/cgi/climatologies.pl).

productivity in this region is regulated by seasonal variation in light available for photosynthesis. Daily net primary productivity varies seasonally in the subarctic waters of the north Pacific, from 0 net productivity for several months at a time in winter, to >0.5 g C/m^2 per day during summer months (Fig. 3; Lalli and Parsons 2001).

The population status of four of the five species of sea lions is either endangered, threatened or in decline (Table 1). Competition with fisheries has been cited as a possible reason for the decline of four of the five species of sea lions (Trillmich and Ono 1991; Mattlin et al. 1998; DeMaster et al. 2001b). The most common type of competitive interaction with fisheries is likely to be a reduction in overall prey biomass as well as localized prey depletion in critical sea lion habitat (DeMaster et al. 2001b). In addition, changes in ocean circulation patterns due to multi-decadal regime shifts may be altering the nutritional value and accessibility of prey to individuals, particularly Steller sea lion populations in the Aleutian Islands (Chavez et al. 2003).

Table 1 Status of sea lion populations throughout the world (Reidman 1990; Angliss and Lodge 2003; Wilkinson 2004).

Species	**Estimated Population Size**	**Status**
Australian Sea Lion (*Neophoca cinerea*)	10,000-12,000	Endangered
New Zealand Sea Lion (*Phocarctos hookeri*)	12,000-16,000	Threatened/Endangered
Steller Sea Lion (*Eumetopias jubatus*)	84,000	Threatened/Endangered
Galápagos Sea Lion (*Zalophus wollebaeki*)	14,000	Threatened
Southern Sea Lion (*Otaria flavescens*)	275,000	Decreasing
California Sea Lion (*Zalophus californianus*)	145,000	Increasing

Population decline and research needs

Steller sea lions have declined by >80% throughout the western portion of their range during the last 30 years. To address the continuing decline (Loughlin and York 2000), the western stock of Steller sea lions was listed as 'endangered' in 1997 under the U.S. Endangered Species Act (ESA). The leading hypothesis for the cause for decline is nutritional stress possibly related to intense commercial fishing activities and environmental changes affecting the available prey base (Alverson 1992; Alaska Sea Grant 1993; Merrick et al. 1997; Calkins et al. 1998). The ecological effects of multi-decadal regime shifts in the Bering Sea and eastern North Pacific, combined with long-term global environmental changes, may have contributed to a reduction in diet diversity for the western population (Pascual and Adkinson 1994; Merrick et al. 1997; Anderson 2001; Chavez et al. 2003). High concentrations of walleye pollock (*Theragra chalcogramma*) in the diet of the declining population correspond with a reduction in Pacific herring (*Clupea harengus pallasi*) and capelin (*Mallotus villosus*) in the available prey base. Diverse prey items are easier to find, capture and handle (Merrick et al. 1997). Bioenergetic modeling indicates that Steller sea lions are required to eat 35% to 80% more pollock than herring to acquire the same energy for metabolic demands (Rosen and Trites 2000).

At the same time these changes in the available prey base were occurring due to environmental factors, post WWII expansion of U.S. ground fish fisheries in Alaska led to an exponential increase in fisheries takes. The walleye pollock fishery in the United States is now the world's largest whitefish fishery and the largest U.S. fishery by volume.

More than one million metric tons of fish is harvested annually from Alaskan waters accounting for more than 30% of the annual U.S. seafood harvest (Marine Stewardship Council 2003). Passage of the Magnuson Fisheries Conservation and Management Act of 1976 (MFCMA) led to increased catches in fall and winter, take of quotas in less time, and concentration of between 50% and 90% of walleye pollock removals in critical habitat for Steller sea lions (Fritz et al. 1995).

With the listing of the western stock of Steller sea lions under the ESA, a piscivorous marine mammal was listed for the first time which has a history of high incidental takes by fisheries and an overlap in diet and distribution with those fisheries (Calkins and Pitcher 1982; Loughlin and Nelson 1986; Perez and Loughlin 1991). Localized prey stock depletion as a result of intensive fishing events, with a subsequent disturbance in prey patch quality and distribution, could be affecting prey accessibility to individuals (Fritz et al. 1995; Shima et al. 2002). Evidence indicates that Steller sea lions target dense aggregations of prey (National Marine Fisheries Service 2001; Sinclair and Zeppelin 2002), and a decrease in the mean density of pollock aggregations may decrease the success rate of sea lion foraging trips.

Foraging ecology

The ways in which predators and prey interact have been examined for central tendencies that can be defined as ‘strategies’. Optimal foraging theory asserts that natural selection will favor individuals that forage ‘optimally’, balancing the costs of different foraging strategies with the nutrients or calories gained (MacArthur and Pianka 1966; Charnov 1976). The particulars of this ‘balancing act’ were refined through the development of

optimality models which provided explicit, quantitative predictions of how animals should behave while foraging (Stephens and Krebs 1986). According to these models, optimal behavior while foraging can include searching for and feeding on prey in an energetically efficient manner (Stephens and Krebs 1986; Mangel and Clark 1986) and reducing the risk of predation while foraging (Lima and Dill 1990).

Central-place foraging theory was developed as a subset of general foraging theory (Schoener 1979; Orians and Pearson 1979). It focuses on predictions regarding how animals will behave when foraging from a central place. The hypotheses were first considered for reproducing birds raising offspring that were likely to return continuously to a nest to feed their young. Questions were raised regarding how these parents would behave given distance from the nest, productivity of prey patches, competition with conspecifics, and predation risk. These questions were developed and then applied to a variety of species acting as central-place foragers, regardless of dependent offspring, with hives, preferred resting locations, or hiding locations defined as central locations from which animals foraged.

Central place foraging theory was first applied to marine animals (particularly otariid seals and birds) in the 1980's when instruments for monitoring the diving and ranging behavior of marine mammals and birds at sea were developed (Gentry and Kooyman 1986). For otariid seals, haul-out locations were considered to be central places from which individuals foraged, and trips to sea were considered to be foraging trips. Analysis of foraging behavior was often restricted to females with dependent offspring, because instruments used to monitor behavior were most likely to be recovered from mothers with pups.

An interesting twist on central-place foraging theory was applied to breath-hold divers (Kramer 1988). This examination of foraging by a diving mammal treated the surface as the 'central place' and the individual dive as the 'foraging trip'. For animals with prey resources at depth, the decision of when to terminate a dive and return to the surface to replenish oxygen stores is likely to affect foraging efficiency and, ultimately, reproductive success. The combination of distance from resting or 'haul-out' locations and depth of prey patches has been used to examine foraging behavior of breath-hold divers (Houston and Carbone 1992; Thompson et al. 1993; Carbone and Houston 1996; Mori 1998a,b; Thompson and Fedak 2001).

This thesis will seek to address specific questions about juvenile foraging behavior of the Steller sea lion through the application of foraging theory. Changes in focus (see definition pg. 2) of juvenile sea lion dive behavior will be used to characterize changes in individual prey accessibility based on optimality theory, optimal foraging and central-place foraging theory.

Research objectives

The objectives of the current study are threefold:

1) To assess effects of 1-3 months of captivity on the ranging and diving ability of juvenile Steller sea lions from the western stock. Effects of captivity on endurance, habitat use, and development of diving and ranging behavior are tested.

2) To develop a new method for assessing individual prey accessibility to juvenile sea lions using focus in time spent at depth.

3) To test the use of focus as a proxy for prey accessibility using specific predictions regarding how focus will vary with season, time of day and foraging trip parameters. Predictions regarding how focus will vary are based on foraging theory, including general optimality theory, optimal foraging theory and central place foraging theory.

In Chapter II the effects of temporary captivity on the diving and ranging behavior of juvenile Steller sea lions are assessed. Hypotheses based on predicted changes in behavior due to temporary captivity, including changes in endurance, habitat use and development, are tested. The behavior of temporarily captive juveniles (spending up to three months in captivity prior to release) is compared with diving and ranging behavior of free-ranging juveniles from this and other studies.

In Chapter III focus is examined; including how to calculate and apply changes in focus in time animals spend at depth and how it compares with other methods of analyzing satellite dive recorder (SDR) data. To review, as defined on page 2, 'focus' is defined as variation in vertical distribution of time spent at depth. It is calculated based on a model distribution of behavior which is developed using the behavior of juvenile sea lions from other studies and optimal predictions of dive behavior. Deviation from the model is assessed and compared with season, time of day and foraging trip parameters. Seasonal and diel variation in focus is examined with depth to determine the sensitivity of this measure to environmental fluctuation. Specific predictions on how focus should vary with changes in foraging trip parameters such as foraging trip distance, duration, and haul-out use and duration are also tested. Chapter IV provides a summary of the findings of previous chapters, overall conclusions which can be made based on the work, and recommendations for further research.

CHAPTER II

DIVING AND RANGING BEHAVIOR OF JUVENILE STELLER SEA LIONS: EFFECTS OF TEMPORARY CAPTIVITY

Introduction

Management of wildlife populations may entail the temporary captivity and release of wild-caught individuals for research, rehabilitation or relocation. The efficacy of rehabilitation and relocation programs can only be assessed through post-release monitoring of individuals (Griffith et al. 1989; Fischer and Lindenmayer 2000; Goldsworthy et al. 2000). Marine mammals and birds are a common focus of rehabilitation and release efforts, whether through long-standing rehabilitation programs or in response to catastrophic events such as oil spills (Estes 1992; Sharp 1996; Wilkinson and Worthy 1999). Many pinniped species are rehabilitated and released through these programs (reviewed by Wilkinson and Worthy 1999). Post-release monitoring that compares the behavior of temporarily captive and free-ranging individuals of the same age class and location, although necessary to determine effects of captivity (IUCN 1998; Britt et al. 2004), is rarely if ever conducted for pinnipeds (Lander et al. 2002).

Reintroduction of individuals to the wild may result in disorientation, inability to re-socialize and locate suitable habitat, and reduced capacity due to physiological or psychological effects of captivity (IUCN 1989; Hull et al. 1998; Goossens et al. 2005).

Effects of captivity on juvenile Steller sea lions may include reduced foraging experience as juveniles develop, lack of physical training due to confinement, and changes in allocation of resources during growth. These effects of captivity may be reflected in such behavioral variables as maximum and cumulative ranging distance, duration of foraging trips and dive depth and duration. It can be predicted that maximum ranging distance, cumulative ranging distance, and dive depth and duration will be reduced in juveniles that experience temporary captivity. In addition, an increase in number of haul-outs used could show a lack of re-socialization or difficulty locating suitable habitat for temporarily captive juveniles.

Lack of juvenile survival has been suggested as one of the driving forces behind an 80% decline in western stock Steller sea lions (DeMaster et al. 2001a) and the subsequent listing of this population as endangered under the U.S. Endangered Species Act. The capture and temporary captivity of Steller sea lion juveniles may be useful for research, rehabilitation or relocation purposes to address the decline. Post-release monitoring of temporarily captive Steller sea lions has been conducted for only a few rehabilitated pups (Lander and Gulland 2003). No behavioral comparison of temporarily captive juvenile Steller sea lions with free-ranging individuals from the same age class and locations is currently available. The Alaska SeaLife Center (Seward, AK) conducts a program for temporary captivity of Steller sea lion juveniles. Juveniles are captured at sea and spend up to 3 months in a captive facility where their mobility is constrained, and where they participate in fasting and feeding trials, health assessments, and other experimental procedures. Movement patterns, dive depths, and dive durations are

compared with those of free-ranging juveniles from the same age class and location, as well as with Steller sea lion juveniles and adults from other studies.

Methods

Juvenile Steller sea lions were captured at known haul-out locations for the western population in Prince William Sound, Alaska and neighboring areas (Fig. 1). All juveniles were estimated to be between 1-3 yrs in age based on tooth eruption patterns, body mass and morphometric measurements (unpublished data. Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Rd., Anchorage, AK 99518), and were captured by SCUBA divers using an underwater noosing technique (McAllister 1998, unpublished report). After one to 3 months in captivity, most temporarily captive juveniles were released in small groups of 2 to 4 at their capture location. If this was not possible due to weather or other constraints, juveniles were released from locations near the captive facility in Resurrection Bay (Cape Resurrection), Alaska. Free-ranging juveniles were released within a few hours of capture at their capture location.

Sea lions were monitored using Satellite Dive Recorders (SDR-T16, Wildlife Computers, Redmond, WA). The SDRs were attached during the final health assessment prior to release using Devcon 5-min epoxy. Devices were attached to the fur along the midline of the back as in Merrick et al. (1994). Data collected by the SDRs include 6-hour histograms of dive depths and durations, time-at-depth, and time spent hauled out or at the surface vs. diving in 20 minute increments for each 24 hour period. Maximum

depths per 24 hour period were also recorded. Location data were obtained using the Argos satellite system and classified for accuracy by Argos. Location class (LC) 3 is the most accurate with accuracy estimated to be within 150 m, and LC 0 is the least accurate with estimated accuracy 1000 m or more (Service Argos 1984; Lesage et al. 1999; Raum-Suryan et al. 2004). For a conservative estimate of ranging behavior comparable with other studies of Steller sea lion juveniles, only location classes 3, 2, 1, and 0 were used in the analysis of ranging behavior after a maximum swim speed filter of 10 km/hr was applied to the location data (Merrick and Loughlin 1997) and locations on land were deleted. Location data were imported into Arcview 3.2 (ESRI, Inc. Redlands, CA) and analyzed using the Animal Movement Arcview extension (Hooge and Eichenlaub 1997). All spatial data were plotted using WGS 1984 datum and re-projected using the Alaska Albers Equal Area Projection.

The SDR-T16 has a depth resolution of 2 m with an accuracy of ± 2 m. Pressure is sampled every 10 s, and dives are characterized with a temporal accuracy and resolution of ± 10 s. The threshold depth for a dive was programmed at 6 m based on diving behavior reported for juvenile Steller sea lions (Loughlin et al. 2003) and the 2 m resolution of the instrument. Depth bins were organized to provide high resolution at shallow depths as average maximum dive depths for juvenile (1-3 yr) Steller sea lions were reported to be shallow (16.6 m; Loughlin et al. 2003). The fourteen depth bins consisted of 6-8, 10-16, 18-24, 26-32, 34-40, 42-50, 52-60, 62-70, 72-80, 82-100, 102-120, 122-160, 162-200, and >202 m, with a resolution of 2 m. Duration bins were organized to provide the highest resolution possible for the instrument (60 s). Dives

were sampled for duration every 10 s. For the first four temporarily captive juveniles, 9 duration bins were programmed to record dives in 60 s increments with the maximum-duration bin recording any dive >490 s (8.2 min). To provide additional resolution for maximum dive duration, ten (10) duration bins were programmed for the remaining 13 juveniles with the deepest bin recording any dive >550 s (9.2 min). Mean dive depths and durations were estimated for each 6-hour period by using the mid-point of the range of each bin and the lowest measurable limit of the deepest or longest bin (i.e., 201 m and 485 s). The mid-point of the range of each bin was multiplied by the number of dives to that bin per 6-hour period. The mean depth and duration of dives per 6-hour period was then calculated. Although binned data do not provide high resolution for individual dives, this method of calculating mean depths and durations from binned data provides comparable results with mean values computed from high resolution instruments such as time-depth recorders (Burns and Castellini 1998) and can be used for comparison with other studies (Merrick and Loughlin 1997; Lander and Gulland 2003; Loughlin et al 2003).

Statistical tests were conducted using SPSS 11.0. Differences between groups were tested using independent or paired samples t-tests. Mann-Whitney U tests were used when assumptions for parametric tests were not met. Estimates of sample size required to conduct parametric statistical tests and analysis of power and effect size were taken from Lehner (1996).

Results

Twelve temporarily captive (TJ001-TJ012) and five free-ranging (JUV001-JUV005) juveniles were monitored as of March 2005, including 8 males and 9 females (Table 2). Juveniles were released in varying seasons and locations, with all free-ranging juveniles released in late July, 2004 in Prince William Sound. All diving and ranging data obtained from juveniles transmitting from September 2003 through March 2005 are included in this analysis. The mean length of transmission for the SDRs as of March 8, 2005 was 69 d (range 12 to 162). Four of the twelve temporarily captive juveniles were re-sighted in apparently good physical condition from a few weeks to 6 months after SDR transmission ceased.

The mean length of transmission for temporarily captive juveniles was 88 d (range 15 to 162 d) and 25 d (range 16 to 52 d) for free-ranging juveniles. Length of SDR transmission varied significantly between the two groups (Z=-2.218, P<0.05). The shorter transmission length for free-ranging juveniles was likely due to attachment of SDRs during the summer months when juveniles were approaching the annual molt. Temporarily captive juveniles tagged during summer also had a reduced average length of transmission of 31 d (range 21 to 40 d). Mean transmission time between summer temporarily captive juveniles and free-ranging juveniles was not significantly different (t=0.695, P>0.05, df=7, eta squared = 0.06).

Table 2 Release data for 17 juvenile Steller sea lions monitored, as of March 2005.

	ID	Sex	Mass (kg)	Standard Length (cm)	Capture location	Release	Transmission length (d)
Temporarily Captive	**TJ001**	M	121	181	Cape Resurrection	Sept. 2003	107
	TJ002	F	104	167	Cape Resurrection	Oct. 2003	15
	TJ003	M	133	184	Procession Rocks	Dec. 2003	137
	TJ004	F	145	196	Procession Rocks	Dec. 2003	137
	TJ005	F	129	179	Glacier Island	May 2004	32
	TJ006	F	140	188	Glacier Island	May 2004	40
	TJ007	F	166	197	Glacier Island	May 2004	32
	TJ008	M	176	199	Glacier Island	May 2004	21
	TJ009	M	134	181	Cape Resurrection	Sept. 2004	146
	TJ010	F	107	176	Cape Resurrection	Sept. 2004	85
	TJ011	M	114	173	Pt. Elrington	Sept. 2004	142
	TJ012	M	135	186	Glacier Island	Sept. 2004	162
Free-ranging	**JUV001**	M	119	176	Glacier Island	July 2004	52
	JUV002	F	99	164	Glacier Island	July 2004	12
	JUV003	F	101	164	Glacier Island	July 2004	16
	JUV004	F	79	157	Glacier Island	July 2004	29
	JUV005	M	99	166	Glacier Island	July 2004	16

Mean estimated maximum ranging distance (± se) from haul-out locations for temporarily captive juveniles was 51 ± 9 km. Mean number of haul-out locations used was 2 (range 1 to 3) and the longest straight-line transit distance was 265 km. Mean

estimated maximum ranging distance from haul-out locations for free-ranging juveniles was 29 ± 9 km. Mean number of known Steller sea lion haul-out locations used was 1 (range 1 to 3) and longest straight-line transit distance was 101 km. Although most temporarily captive juveniles were released in groups of 2 to 4 individuals, location records did not indicate that these juveniles maintained a close association after release. Haul-out locations used by temporarily captive juveniles were typical haul-out locations for the population and did not differ from haul-out locations used by free-ranging juveniles. Five of the 12 temporarily captive juveniles made long-range transit trips to new haul-out locations of >118 km. Four of the five trips were initiated or conducted within the first few weeks after release by 3 females and one male juvenile, with the longest straight-line transit trip of 265 km conducted by a female from her capture location at Resurrection Bay to Cape St. Elias (Fig. 4). All but two of the temporarily captive juveniles were released at their capture locations. Of these two, both made movements back toward their capture locations then returned to the release location within 30 days.

There was no significant difference in mean estimated maximum ranging distance from haul-outs between temporarily captive and free-ranging juveniles (t=1.661, P>0.05, df=12.526), although the magnitude of the difference between the means of the two groups was large (eta squared=0.20). Haul-out use also did not differ significantly between the two groups (Mann-Whitney U, *ns*).

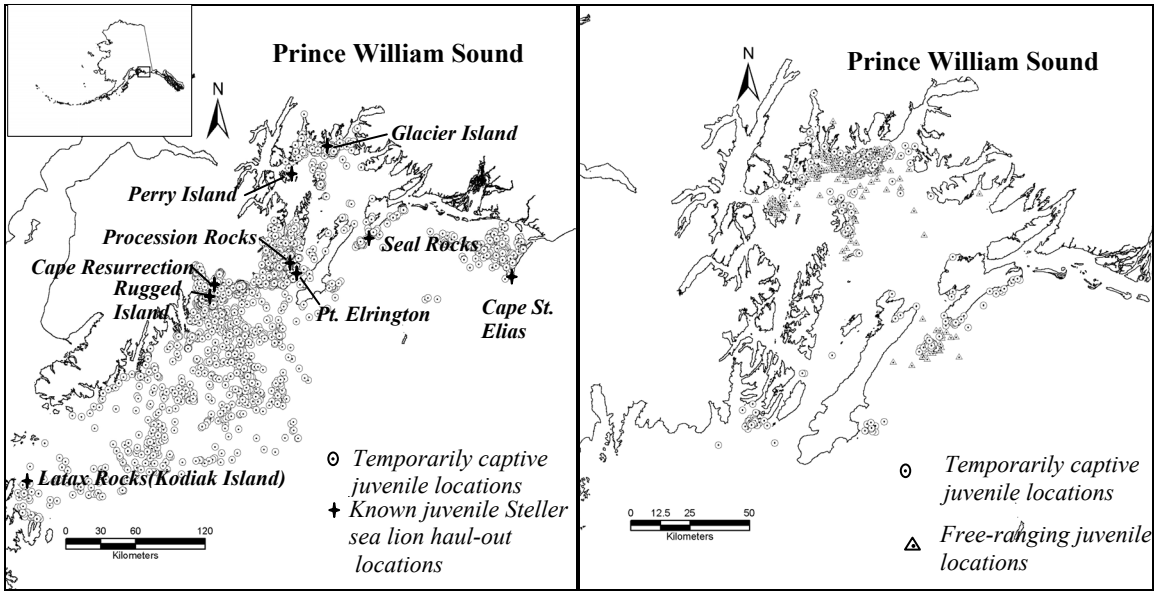


Fig. 4 At-sea and haul-out locations for **(a)** temporarily captive juvenile Steller sea lions monitored from September 2003 through March 2005 in Prince William Sound, Alaska and **(b)** temporarily captive and free-ranging juvenile locations monitored during Summer 2004.

Spearman's rank-order correlation (*rho*) was used to calculate the strength of the relationship between mean maximum ranging distance from haul-outs, number of haul-outs used and length of transmission. There was a significant positive correlation between length of transmission and average maximum ranging distance (n=17, P<0.05) with length of transmission explaining 25 percent of the variance in average maximum ranging distance (r_s=0.495). Length of transmission and number of haul-outs used were also significantly correlated (n=17, P<0.05), with length of transmission explaining 32 percent of the variance in number of haul-outs used (r_s =0.567).

To reduce effects of seasonal variability and length of transmission on ranging behavior, a comparison of mean ranging distance was conducted between free-ranging

(29 ± 9 km, n=5) and temporarily captive juveniles monitored in summer (40 ±13 km, n=4). No significant difference was found between the two groups in mean estimated maximum ranging distance from haul-outs (t=1.034, P>0.05, df=7) although 13 percent of the variation in ranging distance was explained by group (eta-squared=0.13).

To assess initial effects of temporary captivity on ranging behavior, total cumulative distance traveled was estimated for each temporarily captive juvenile for the first 7 days of transmission and compared with the next 7 days of transmission. The mean (± se) cumulative distance traveled for temporarily captive juveniles was 104 ± 19.5 km for the first seven days and 127 ± 18.5 km for the next seven days. No significant difference was found between the ranging behavior in the first seven days when compared with the next seven days (t=-0.769, P>0.05, df=11, eta-squared=0.05).

Mean dive depth and duration (± se) were calculated for each juvenile using the mean depths and durations for each 6-hour period of histogram data. Mean depth and duration were significantly deeper and longer for temporarily captive juveniles than for free-ranging juveniles (t=2.665, P< 0.05, df=13 and t=2.842, P<0.05, df=14). Mean depth and duration (± se) for temporarily captive juveniles were 33.7 ± 21.2 m and 99.1 ± 34.6 s. Mean depth and duration for free-ranging juveniles were 16.5 ± 2.0 m and 68.6 ± 4.0 s. There was no significant difference in either mean depth or duration for temporarily captive versus free-ranging juveniles monitored in summer (t=-1.675, P>0.05, df=6.725, eta-squared = 0.29 and t=-0.456, P>0.05, df=7, eta-squared =0.03). Mean depth and duration (± se) for temporarily captive juveniles monitored during summer months were 13.1 ± 0.5 m and 66.3 ± 5.5 s. The lack of significant difference

found for depth during summer is likely due to a lack of statistical power, as 29 percent of the variance in depth for juveniles monitored in summer was explained by group. Only 3 percent of the variation in mean dive duration was explained by temporarily captive versus free-ranging status of the juveniles.

To assess effects of captivity on dive depth or duration for temporarily captive juveniles, the mean depth and duration (±se) were compared for the first and second seven days after release. Mean dive depth and duration for temporarily captive juveniles for the first seven days after release were 13.6 ± 3.6 m and 65.7 ± 14.4 s. Mean dive depth and duration for the next seven days after release were 18.8 ± 6.9 m and 74.8 ± 17.1 s. Mean depth and duration were significantly deeper and longer during the second week after release (t=-3.524, P<0.01, df=11 and t=-2.524, p<0.05, df=11).

The mean (± se) daily maximum dive depth reached by temporarily captive juveniles was 101.0 ± 43.1 m versus 43.5 ± 16.0 m by free-ranging juveniles. Mean daily maximum dive depth was significantly deeper for temporarily captive juveniles than for free-ranging juveniles (t=3.893, P<0.01, df=14.955). Mean daily maximum dive depth of 58.0 m ± 14.0 reached for temporarily captive juveniles diving in summer was not significantly deeper than mean maximum daily dive depth for free-ranging juveniles (t=1.327, P>0.05, df=7), although 20 percent of the variation in maximum daily dive depth was explained by group (eta squared = 0.20). Maximum dive depths are likely to be affected by the aerobic dive limit of juveniles which is closely tied to body oxygen stores or mass (Schreer and Kovacs 1997). During summer, mean mass (± se)

was significantly greater for temporarily captive juveniles (152.8 kg ± 21.9, n=4) when compared with free-ranging juveniles (99.4 kg ± 14.2, t=4.440, P<0.01, df=7).

All twelve temporarily captive juveniles engaged in dives of at least 5.2 min in duration within the first two weeks after release with the exception of one female (TJ002) which never undertook a dive longer than 5.2 min, although she was diving for >4.2 min within the first day after release. Within the first two weeks after release, all twelve temporarily captive juveniles were diving to depths greater than 50 m (range 50 – 240 m). The deepest dive depth as of March 2005 was 432 m recorded for a male temporarily captive juvenile (TJ003) during December 2003 in the first month after release. Maximum dive durations for juveniles were >8.2 min for two temporarily captive male juveniles released in winter (TJ003 and TJ011) and >9.2 min for two temporarily captive females released in summer (TJ005 and TJ007). These maximum dive durations occurred within the first month after release for three of these four temporarily captive juveniles.

Discussion

Initial post-release monitoring of temporarily captive juveniles did not indicate any effects of captivity on ranging behavior. Movements from haul-out locations as well as long range trips were consistent between temporarily captive and free-ranging juveniles. The lack of significant differences in ranging behavior between the two groups may have been obscured by small sample size; however, there was no indication that temporary

captivity reduced the ability of juveniles to locate and move between usual haul-out locations for juvenile Steller sea lions. The lack of a difference in the cumulative distance traveled between the first and second weeks for temporarily captive juveniles indicates that, at least within the first two weeks, ranging ability was not impaired. In addition, long-range trips conducted by temporarily captive juveniles within the first few weeks of release indicate that juveniles were able to freely locate and make use of suitable habitat. When compared with juveniles from other studies, temporarily captive juveniles did not exhibit reduced ranging ability (Table 3). Average number of haul-outs used for temporarily captive juvenile Steller sea lions were consistent with haul-out use reported for western stock juveniles in other studies (Raum-Suryan et al. 2002, 2004) and did not indicate restricted movement of temporarily captive juveniles. This result also suggests that number of haul-outs used did not increase due to disorientation or inability to locate preferred habitat upon release. The average length of transmission for juveniles in Raum-Suryan et al. (2004) was also comparable with length of transmission time for temporarily captive juveniles in this study.

The consistently longer and deeper dives conducted by temporarily captive juveniles when compared with free-ranging juveniles were likely a result of seasonal differences in behavior. The lack of significant difference in mean duration of dives between the two groups when compared within the same season is the best indication of lack of effect of captivity on average diving ability for temporarily captive juveniles. Changes in dive duration are a good indicator of diving development for juvenile otariid seals (Horning and Trillmich 1997) and can be more responsive to juvenile diving ability

than changes in depth (Burns et al. 1997). Long (>4.2 min) dive durations performed by all 12 temporarily captive juveniles within the first few weeks after release also indicate no reduced diving performance due to temporary captivity.

Table 3 A comparison of diving and ranging behavior for Steller sea lions reported from this and other studies.

Source	Mean Depth (m) ± se	n	Mean duration (s) ± se	Ranging behavior (km) ± se	Mean daily max dive depth (m)	Max dive depth (m)	Max dive dur (min)	Mean # days trans (d)
Temporarily Captive Juveniles (this study)	33.7±21.23	12	99.1±34.56	51±9[a] (max 265)	101±43.09	432	>9.2	88 (range 15-162)
Free-Ranging Juveniles (this study)	16.5±2.03	5	68.6±3.95	29±9[a] (max 101)	43.5±15.94	108	>4.2	25 (range 16-52)
Merrick and Loughlin 1997 (young of the year)	9 (median)	5	60 (median)	30±14.5[b]	NR	72	>6	41
Merrick and Loughlin 1997 (adult females summer and winter)	21 and 24 (medians)	9	78 and 120 (medians)	17±4.6 and 133±59.9[b]	NR	>250	>8	17 and 85
Lander and Gulland 2003 (young of the year)	22.60±6.42 (sd)	3	67.8±24 (sd)	NR (max 850)	NR	220	>9.5	~80 (range 30-120)
Loughlin et al. 2003 (western stock juveniles)	16.6±11.01 (sd)	5	66±25.05 (sd)	24.6[b]* (max 342)	63.4±18.93	288	>6	61 (range 40-94)
Raum-Suryan et al. 2004 (eastern and western stock juveniles and young of the year)	ND	103	ND	90%≤15[b] (max 1,300)	ND	ND	ND	82.8±5.9 (se)
Briggs 2005 (western stock yoy/ juveniles)	10.75	15	60.4	3-15 km offshore	193	592	>3	122 (range 38-181

ND=no data, NR=not reported. a. Mean estimated maximum ranging distance from haul-outs based on 50% kernel home-range analysis, Animal Movement extension, Arcview 3.2. b. Mean individual trip length. * Value for all temporarily captive juveniles from study (n=12)

Reduced mean mass of free-ranging juveniles when compared with temporarily captive juveniles from the same season may have confounded the comparison between free-ranging and temporarily captive juveniles with regard to daily maximum dive depth. However, two of the temporarily captive juveniles released in summer made some of the longest dives reported for juvenile Steller sea lions (Table 3) within the first few weeks after release, which does not indicate that diving performance was impaired by captivity. The reduced duration and depths of dives for juveniles released in summer likely reflect seasonal variation in behavior rather than reduced diving ability.

Differences in mean diving depth and duration between the first and second week after release show development in diving behavior over time for temporarily captive juveniles. The performance of deep, long dives within the first few weeks by all 12 temporarily captive juveniles could indicate that increases in mean dive depth and duration during the first two weeks are a result of increased foraging behavior by juveniles as nutritional stores obtained during captivity are lost, rather than increased diving performance due to effects of captivity. Regardless, mean dive depths and durations for temporarily captive juvenile Steller sea lions during the first week after captivity are well within the range reported for free-ranging juvenile Steller sea lions from other studies (Table 3).

Temporarily captive juvenile mean dive depths, mean dive durations, and maximum daily dive depths consistently exceeded previously reported mean values for juveniles and even adults from western stock Steller sea lions (Table 3). Long-term effects of temporary captivity on survival and reproduction were not monitored in this

study. However, short term monitoring of behavior during the first weeks to months after release does not indicate any effects of temporary captivity on diving and ranging behavior or haul-out use. As measures continue to be taken to address the decline of western stock Steller sea lions, this study indicates that bringing wild-caught juvenile Steller sea lions into temporary captivity is a viable option for management or research purposes.

CHAPTER III

FOCUS IN FORAGING BEHAVIOR OF JUVENILE STELLER SEA LIONS AS AN INDICATOR OF PREY ACCESSIBILITY

Introduction

The response of individual predators to a change in prey accessibility may range from slight changes in behavior to failure to reproduce (Kramer 2001). To maximize efficiency, a diving predator can maximize the rate of energy gain versus energy expenditure over different time scales--from individual dives, to foraging trips, to seasonal foraging effort (Kramer 1988; Mori 1998a,b; Cornick and Horning 2003; Thompson and Fedak 2001). Prey accessibility can be described as the availability of a prey item or prey patch to an individual. This availability is determined by the behavior and distribution of prey as well as the behavior of the predator (see Chapter I, page 2). Prey encounter rates, along with prey handling and capture efficiency, greatly affect foraging costs. Although prey distribution can be measured at the meso-scale, fine-scale prey distribution and its subsequent effect on individual foraging success are difficult to assess in free-ranging conditions.

Relating the behavior of a predator to the density distribution of its prey is an important aspect of foraging theory. Predators foraging on clumped or patchy prey items which are horizontally and vertically aggregated are likely to show increased focus

in their foraging behavior. To review, 'focus' is defined as the vertical concentration in space of a predator's diving behavior. (See Chapter I; page 2 and methods section, this chapter). Predators foraging on dispersed prey that are more evenly distributed in space should show behavior that is also less focused or highly dispersed. The marginal value theorem has been applied to foraging theory to derive a 'giving-up rule', assuming that a forager will remain within a prey patch until the density of prey becomes consistent with the average density of prey in the environment (Charnov 1976; Parker and Stuart 1976). For diving animals, prey-patch quality cannot be estimated until the depths are reached at which prey occur. A simple rule-of-thumb approach was postulated for diving animals which assumes that they will abandon dives where no prey are encountered before some threshold time for the dive has been reached (Thompson and Fedak 2001).

Diving mammals are under the unique constraint of availability of oxygen during foraging. According to optimal foraging models for diving predators, fine-scale changes in prey distribution influence foraging efficiency (Kramer 1988; Ydenberg and Clark 1989; Houston and Carbone 1992; Thompson et al. 1993; Carbone and Houston 1996; Mori 1998a,b). The decision to terminate foraging, whether at the spatial and temporal scale of individual dives, particular prey patches or larger foraging habitats may also be related to prey accessibility (Ydenberg and Clark 1989; Horning and Trillmich 1999; Thompson and Fedak 2001). Some diving predators will forage closer to the surface, even though the highest density of prey patches remains below the maximum depth of their dives (Benoit-Bird and Au 2003). Decisions by breath-hold foragers are then a

trade-off between the density, quality and behavior of prey, distance from the surface, and in the case of pinnipeds, distance from haul-out locations.

The rates at which individuals encounter, interact with, and consume prey have been inferred (Croxall et al. 1988; Costa et al. 1989; Boyd 1996) and measured (Davis et al. 2003) for marine mammals from information obtained from dive profiles. Behavioral variables, such as number of dives per hour or duration of foraging trips, have also been used to quantify foraging behavior (Horning and Trillmich 1997). Within the spatial and temporal scale of an individual dive, many factors can contribute to observed behavior. Duration of dives, number of dives, median and maximum depth of dives, and time spent at the surface may indicate physiological limitations of the individual or changes in fine scale prey distribution. Diving animals can expand their foraging range both horizontally, by increasing trip length and foraging area, and vertically, by increasing the depth of dives.

Use of the water column by diving sea lions is reflected in time-at-depth data collected from satellite dive recorders (SDRs). An examination of dive characteristics of sub-adult and adult harbor seals (*Phoca vitulina*) in Prince William Sound indicated that a significant proportion of dive time is spent at particular "focal depths" (Frost et. al. 2001) . These focal depths may reflect use of specific portions of the water column for foraging and may also indicate accessibility of prey from the surface to a diving predator.

Pinniped dives have been categorized into different 'types' using data collected from time-depth recorders. "V"-shaped dives have been described as transit or searching

dives, whereas “U” or “square” shaped dives, with a significant portion of the dive time spent at the bottom of the dive, have been classified as foraging dives (Lesage et al. 1999; Le Boeuf et al. 2000; Thompson and Fedak 2001). Individual dive profiles analyzed for time-at-depth revealed an increase in focus in time-at-depth profiles from individual “U-shaped” dives. “V”-shaped diving returned individual time-at-depth profiles which were less focused and spread throughout the water column (Fedak et al. 2001).

The amount of time animals spend searching for prey necessarily increases as prey density decreases (Thompson and Fedak 2001). Foraging efforts that are spread throughout the water column are more likely to include a higher proportion of search time. Once likely prey sources have been located, focused diving to these particular depths or locations is more likely to allow predators to forage efficiently. Prey accessibility could therefore be indicated by the degree of vertical focus in diving behavior, given the assumptions that (1) increased density of prey items or prey patches is reflected as increased focus in sea lion behavior and (2) increased density of prey items or prey patches in the water column leads to increased prey availability per unit effort. The degree of vertical focus (see Chapter I, page 2) in the water column exhibited by juvenile Steller sea lions at varying spatial and temporal scales may then be used as an indicator of individual prey accessibility.

This new approach to assessing individual prey accessibility based on vertical diving focus can be used to:

- Compare seasonal and ontogenetic trends in prey accessibility within individuals;
- Compare prey accessibility between individuals with seasonal and annual fluctuations in prey distribution and ontogenetic differences;
- Compare prey accessibility by way of observed behavior for different foraging trips, before and after intensive fishing activities, and in different habitat types.

The current study will compare seasonal changes in focus between individuals, changes in focus with depth by season and time of day, and differences in focus within and between individuals with changes in foraging trip parameters to test the use of focus as an indicator of prey accessibility.

Juvenile foraging behavior

Most previous research on the foraging behavior of otariids has examined lactating females with dependent pups. In a study of seasonal differences in female Steller sea lion foraging behavior, trip duration was thought to be affected by the presence of a dependent pup (Merrick and Loughlin 1997). The foraging effort of females should be higher in winter than in summer, due to a seasonal reduction in prey availability, leading

to increased duration of foraging trips. The constraint of a dependent pup was thought to decrease the foraging trip duration of some individuals released in winter. The lifetime reproductive success of a female is related to the survival of her offspring. For a juvenile, reproductive success is dependent only upon surviving to reproduce. Examining the behavior of juveniles, particularly as it relates to foraging trip duration, will remove the constraint on foraging trip duration of a dependent pup and provide new insight into the foraging behavior of otariids.

Juvenile Steller sea lions (age 1-3 yrs) are not constrained by nursing or a dependent pup to return to the same haul-out location and have been characterized as 'multiple central place foragers' (Raum-Suryan et al. 2004) that travel between a limited number of central places (McLaughlin and Montgomerie 1989). The selection of haul-out or 'resting' locations by juveniles may be based solely on relative nearness to foraging sites. As prey availability changes due to movement of prey patches or changes in prey patch concentration, there are relatively few limits on juveniles' ability to move with prey to new haul-out locations or give up on foraging locations with reduced prey availability.

When do juvenile Steller sea lions 'give up'? Testing foraging trip predictions based on optimal foraging theory

When do juvenile Steller sea lions 'give up' during foraging? Proper selection of giving up time should increase overall foraging efficiency if prey accessibility is variable and prey patches are depleted throughout the course of a foraging trip (Charnov 1976). Under these circumstances, returning to a haul-out location to wait until prey availability increases, or alternatively, transiting to a new foraging location where prey availability may be better, will increase the overall foraging efficiency of a predator. Juvenile Galapagos fur seals (*Arctocephalus galapagoensis*) cease foraging and remain hauled-out when prey accessibility is reduced (Horning and Trillmich 1999). Juvenile sea lions in the Gulf of Alaska can 'give up' at varying scales including during an individual dive, during a foraging trip, or at a particular foraging location. When do juvenile sea lions cease foraging efforts and return to haul-out or transit to new locations? Are there foraging trip characteristics that may predict this behavior? If these characteristics can be defined, juvenile behavior can be examined with changes in habitat, season, and before and after intensive fishing activities to see how these variables influence 'giving up' behavior.

Variation in focus with season and time of day

Steller sea lion diets are related to the temporal and spatial distributions of spawning and migrating aggregations of prey species near-shore (Sinclair and Zeppelin 2002). Prey species taken in winter are more diverse and located deeper in the water column and further offshore (Springer 1992; Sinclair and Zeppelin 2002). Important winter prey for Steller sea lions include Pacific cod (*Gadus macrocephalus*) and Pacific herring (*Clupea pallasi*) (Sinclair and Zeppelin 2002). Important summer prey include Pacific salmon (*Oncorhyncus*) and Arrowtooth flounder (*Atheresthes stomias*, Sinclair and Zeppelin 2002). Walleye pollock (*Theragra chalcogramma*) makes up a substantial proportion of Steller sea lion diet in both winter and summer (Pitcher 1981; Frost and Lowry 1986; Springer 1992; Merrick et al. 1997; Calkins 1998; Sinclair and Zeppelin 2002). Sea lions taking more diverse prey located further from shore and deeper in the water column are likely to show reduced focus in winter as individuals respond to reduced prey accessibility.

In response to changes in the behavior and distribution of summer prey, juveniles may increase their foraging effort at night. Schooling prey near shore are likely to migrate vertically toward the surface at night. When examining the dive frequencies of female Steller sea lions in winter and summer, Merrick and Loughlin (1997) found a significant diel pattern in dive frequency with time of day. Females foraging in summer were making more dives per hour during the night (2100 to 0300). Loughlin et al. (2003) also found an overall higher dive frequency at 2100 to 0300 hours

for juvenile Steller sea lions. If prey are located at depth during the long summer days in Alaska, it is likely that the brief night will bring prey closer to the surface and more easily accessible to Steller sea lions. Juveniles should show increased focus at shallow depths in the water column during the brief summer nights if this is the case, and if degree of focus is indeed linked to prey accessibility.

Fish species in the Gulf of Alaska are known to migrate to depth as both hours and intensity of sunlight are reduced in winter, causing a decrease in both primary productivity and cues for initiation of vertical migrations (Springer 1992; Sinclair and Zeppelin 2002). If diel vertical prey migrations are shifted or reduced in Alaska in winter months, it is likely that other factors will regulate diel variation in foraging behavior for sea lions. Lactating female Weddell seals (*Leptonychotes weddelli*) increase the depth of foraging dives as energy reserves are depleted (Sato et al. 2002). Antarctic fur seals (*Arctocephalus gazella*) also increase the depth of dives when prey accessibility is experimentally reduced (Boyd et al. 1997). An increase in focus at depth is also likely for juvenile Steller sea lions if they increase the depths at which they dive as a response to overall reduction in prey accessibility. Antarctic fur seals are known to increase the depth of their dives with increasing light levels (Boyd et al. 1994). If light is a limiting factor in locating and capitalizing on prey sources for sea lions in winter, it is likely that juveniles will show more focus in dive behavior during the limited daylight hours in winter months.

Based on the considerations outlined above, I hypothesize that if focus is an indicator of prey accessibility, *focus will vary with season and time of day* in the following ways:

1. Diving behavior will be more focused in summer than in winter.
2. Diving behavior will show more focus at depth in winter.
3. Diving behavior will show more focus during the day in winter.
4. Diving behavior will show more focus closer to the surface in summer.
5. Diving behavior will show more focus at night during the summer.

Variation in focus with changes in ranging and diving behavior

Individuals that are subject to reduced prey availability are likely to increase both their horizontal and vertical search effort. Female Steller sea lions expand their foraging area both vertically and horizontally during winter (Merrick and Loughlin 1997). In this case, a lack of focus vertically may be correlated with a lack of focus horizontally. Individuals that are having difficulty finding prey are likely to increase their search radius from a haul-out location per individual foraging trip. A lack of focus in diving behavior may be correlated with maximum trip distance of foraging trips from haul-out locations.

In addition to increasing the horizontal distance traveled from a central place, individuals can increase the duration of time spent away from haul-outs searching for

prey. This increase in trip duration is expected with a decrease in prey accessibility. Female Antarctic fur seals were found to increase foraging trip duration when prey availability was experimentally reduced by increasing the cost of locomotion (Boyd et al. 1997). In other studies of lactating female seals returning to a central place from foraging trips, trip duration was often the best indicator of reduced prey availability (Gentry and Kooyman 1986; Costa et al. 1989; Boyd et al. 1994; Walker and Boveng 1995; Thompson et al. 2003). If focus is an indicator of prey accessibility, individuals with reduced focus should show increased trip duration.

Haul-out duration for otariid seals has been examined during periods of low prey accessibility. Galapagos fur seal juveniles increase haul-out duration at times of low prey accessibility (Horning and Trillmich 1997). Trip distances, haul-out duration, and trip duration increased during periods of low prey availability for South American fur seals (*Arctocephalus australis*, Thompson et al. 2003). Juveniles experiencing difficulty finding prey close to haul-out locations may increase haul-out duration. The thermal costs of being at sea, along with increased risk of predation, should lead to an increase in haul-out duration if increased time in the water will not yield a benefit to the individual. This measure of 'resting' behavior could be important as an indicator for when juveniles are not finding prey sources that are either easily locatable or aggregated. Subsequent haul-out duration is likely to vary with variation in focus of foraging trips, although it may also be related to foraging trip duration and distance covered during a foraging trip.

To increase home range size, juveniles may make use of many haul-out locations. Juvenile Steller sea lions are known to use both single and clustered haul-out

locations (Raum-Suryan et al. 2004). Steller sea lion females monitored in winter had larger overall home range sizes than females monitored in summer (Merrick and Loughlin 1997). In general, home range size is likely to be a function of the productivity of a foraging area (Lindstedt et al. 1986). As home range increases with decreasing productivity, juveniles are likely to increase the number of different haul-out locations used. If prey accessibility is driving transit behavior, juveniles finding localized prey sources are less likely to transit to new foraging locations.

According to optimal foraging theory, predators should cease foraging on a prey patch or in a particular location when energy gained is less than energy expended to search for and handle prey items (Charnov 1976; Stephens and Krebs 1986). Variability in foraging trip behavior can be measured and used to predict whether juvenile sea lions will cease foraging and remain in a particular location, or cease foraging and move to a new location. The adoption of a cease-foraging and sit-and-wait strategy in the same location could be a result of either satiety (the juvenile has ingested enough prey to return to haul-out for digestion and to reduce energetic loss due to swimming or thermal demands) or 'giving-up' due to prey patch depletion or a temporary reduction in fine-scale prey availability. It can be assumed that if the second is the purpose of a cessation in foraging, then a number of foraging trips with these same indicators will lead to transit to new foraging locations. If juvenile sea lions transit to new haul-out locations to make use of near-by prey sources, they should show reduced focus prior to transiting to a new location.

Based on these considerations, I hypothesize that if focus is an indicator of prey accessibility, *focus will vary with changes in ranging and diving behavior*. I predict focus will vary with ranging distance in the following ways:

1. Degree of focus will be inversely related to number of haul-outs used; with individuals exhibiting more focus using fewer haul-outs.
2. Degree of focus will be inversely related to maximum distance of foraging trips; with individuals exhibiting more focus traveling less far from haul-out locations.
3. Focus during a foraging trip will be inversely related to distance traveled.
4. Individuals will show reduced focus prior to transiting to a new haul-out location.

I predict that focus will vary with duration of foraging trips and haul-out duration in the following ways:

1. Degree of focus will be inversely related to trip duration; with increased focus leading to reduced overall trip duration.
2. When compared within an individual, longer foraging trips will be less focused than shorter trips.
3. Degree of focus will be related to haul-out duration; with decreased focus leading to longer overall haul-out duration.
4. Within an individual, increased focus during a foraging trip will result in longer subsequent haul-out duration.

Methods

Dive behavior of 17 juvenile (age 1-3 yr) Steller sea lions released in the Gulf of Alaska (60°N, 149°W) in varying seasons and locations was analyzed for focus. See Chapter II for details of capture method, satellite dive recorder (SDR-T-16) instrument description, device attachment and data collection format. All data were recorded in 6-hour histogram periods corresponding to the following times of day: morning (0300-0900), mid-day (0900-1500), evening (1500-2100), and night (2100-0300) local time. Local time was defined as local longitudinal time (Wildlife Computers 1997). All duty cycles started at midnight GMT with an offset of ±13 h for Alaska. Two juveniles released in December had an offset of GMT ±12 h to compensate for changing light levels during winter months.

Data collected by the SDRs included 6-hour histograms of time-at-depth, and time spent hauled out or at the surface versus diving in 20 minute increments for each 24 hour period. Time-at-depth data were collected in 8 depth bins: 0-8, 10-16, 18-24, 26-32, 34-40, 42-50, 52-60, and > 62 m. Time-at-depth data were collected at 10 second intervals with depth resolution of 2 m.

Location data and foraging trip calculation

Location and dive behavior were extracted from the SDR-T16 data using Satpak 2003 (Wildlife Computers, Redmond, WA). Location data were obtained using the Argos

satellite system and classified for accuracy by Argos (Service Argos 1984). Location class (LC) 3 is the most accurate, with accuracy estimated to be within 150 m; and, LC 0 is the least accurate, with estimated accuracy 1000 m or more (Service Argos 1984). Location class A is not classified for accuracy by Argos, but accuracy has been measured at uncertainties less than that of LC 0 (Britten et al. 1994; Brothers et al. 1998; Vincent et al. 2002; Raum-Suryan et al. 2004). Location classes 3, 2, 1, 0 and A were used in the analysis of ranging behavior after a maximum swim speed filter of 10 km/hr was applied to the location data (Merrick and Loughlin 1997) and locations with a Keating Error Index >25 were deleted (Keating 1994; Raum-Suryan et al. 2004). Locations found to be on-land were also deleted. Location data were imported into Arcview 3.2 (ESRI, Inc. Redlands, CA) and analyzed using the Animal Movement Arcview extension (Hooge and Eichenlaub 1997) and pathfind.avx (Jennes 2005). All spatial data were plotted using the WGS 1984 datum and re-projected to local Universal Transverse Mercator (UTM). Foraging trips and haul-out durations were characterized using timeline data which reports time on-land versus at-sea in 20 minute increments.

Individual trips to sea were measured using a minimum of 3 at-sea locations per foraging trip. The location of the furthest distance from the most recent haul-out location was measured for maximum over-water distance. For trips in which individuals transited directly to new haul-out locations, the minimum straight line, over-water distance to the new haul-out location was measured in Arcview. For trips in which sea lions spent time at sea and returned to different haul-out locations, the minimum straight line, over-water distance between the last haul-out location and the furthest at-sea

location was measured and then added to the distance from that location to the next haul-out location used.

Haul-out locations were determined using locations obtained during haul-out periods as characterized by the timeline data, with one at-sea location within 5 km of established haul-out locations for juvenile Steller sea lions or > 3 locations for less established/new haul-out locations identified for juveniles. An individual trip to sea was defined as starting 10 minutes after the last 20 minute period spent on land and ending 10 minutes after the last 20 minute period spent at sea according to time-line data. A trip was not considered to have ended unless the subsequent time spent at the surface was >3 hours, to account for time resting at the surface or brief hauling-out behavior during foraging trips. Transit trips were defined as movements between haul-out locations where more than 3 hours were spent hauled-out at the new location. Parameters associated with trips to sea, including maximum over-water distance traveled, were only measured for trips > 8 hours in duration.

To further test the relationship between focus and foraging trip duration, the longest and shortest foraging trips were compared for each individual with respect to focus. Trips were selected based on the additional descriptive data available, with the shortest and longest round-trip foraging trip having the most additional descriptive data (including trip distance and subsequent haul-out duration) chosen for each individual. Shortest trips were also at least 8 hours in duration. To evaluate focus prior to a transit trip, focus was calculated for the two days prior to the trip and compared with focus for

the 3 through 5 days prior to the trip. These calculations were only made for trips which commenced after a minimum of 7 days spent in the same location prior to transit.

Calculating time-at-depth focus

Focus during a 6-hour period was calculated by first combining the total minutes spent below 9 m. These "total minutes" were calculated from the 6-hour binned time-at-depth (TAD) data in which counts were made to each of 7 bins used by the juvenile at 10 s intervals. The instrument increases the count in a bin by one integer every 10 seconds if the juvenile is located within that time-at-depth bin (for example within the range of 9-17 m for the first TAD bin). Once the maximum number of counts for the instrument is reached in any one bin (255 counts) the instrument automatically adjusts the counts in each bin to compensate for additional counts in any bin. Therefore, the number of counts in each bin can ultimately be used to determine the amount of time spent under conditions corresponding with each bin during a 6-hour period. This is done by calculating the percentage of time spent in correspondence with each bin using the counts for each bin divided by the total count for the 6-hour period, and then multiplying this percentage by 6 hours (360 min). Only 6-hour periods in which the animal spent at least 30 minutes below a depth of 9 m were used for analysis of focus as these were time periods when a juvenile was most likely to be actively feeding or searching for prey.

In order to determine focus versus lack of focus in diving behavior, it is first necessary to determine what percentage of time a juvenile would spend in each time-at-depth bin if diving behavior was not focused. Using similar instruments to those employed in this study, Loughlin et al. (2003) reported the distribution of dives to different depths for nine juvenile Steller sea lions > 1 year of age in various seasons and habitats in Alaska. The distribution of maximum dive depths for juveniles was used to calculate the expected number of dives to each depth bin for this study. Ten hypothetical foraging trips were simulated in which a juvenile made 100 dives per trip. These 100 dives were assigned randomly to focal depths between 9 m and 161 m (98% of all dives for this study had a maximum depth less than 161 m), with the constraint that the percentage of dives occurring in each bin reflected dive distribution data reported for juvenile Steller sea lions >1 year in age (Loughlin et al. 2003). The expected duration for each randomly generated dive was calculated using an equation derived from average dive depth and duration data reported for juvenile Steller sea lions (Loughlin et al. 2003; dive duration = 0.0035 x dive depth + 0.4773, $R^2 = 0.83$). An upper limit of 245 s for dive duration was imposed as 95% of all dives were <4.08 minutes (245 s).

Vertical travel time from the surface to the threshold depth for the focal bin was calculated for each dive using a vertical travel rate of 2.1 m/s, or the travel rate with the minimum cost of transport (MCOT) calculated for juvenile Steller sea lions (Rosen and Trites 2002). This travel time to and from the bin was then subtracted from each dive and the remaining time for each dive was assumed to be spent within that bin. To correct for artificial inflation of bins above the 'focal bin' for each dive, the time spent in

each bin due to vertical travel through that bin was calculated for all 100 dives per trip. This travel time was added to each bin to adjust the expected time spent for that bin.

The expected time spent in each bin per foraging trip was calculated using these adjustments for all 10 hypothetical foraging trips and then used to estimate an expected percentage of time spent in each bin if behavior was NOT focused: 14.73 % in Bin 1 (10-16 m), 16.58% in Bin 2 (18-24 m), 9.52% in Bin 3 (26-32 m), 9.64% in Bin 4 (34-40 m), 10.42% in Bin 5 (42-50 m), 4.69% in Bin 6 (52-60 m), and 34.42% in Bin 7 (62-162 m). The model does not predict a normal or uniform distribution for time spent in each TAD bin for juveniles in this study. Rather, juveniles are expected to exhibit a roughly binomial distribution in TAD, with more time spent in the two shallow depth bins and the deepest TAD bin due to the width of the bins, behavior of juveniles from other studies, and the travel time to and from each bin. For comparisons of changes in focus with ranging behavior, "maximum focus" was defined as the percent time observed minus expected in the time-at-depth bin with the greatest focus, or the greatest positive difference from expected behavior.

Another method for determining focus in the water column using SDR data was described in Frost et al. (2001). This method uses the maximum depth of dives as counts in each depth bin to determine the "focal depth" for that dive, rather than time-at-depth data used in the current study. Using the dive counts per bin for each 6-hour period, Frost et al. (2001) calculated focus using Simpson's Diversity Index. This method relies upon the number of counts in each bin as an indicator of focus (F) in that bin, such that the maximum value for focus is 1 (all dives were to the same bin). If dives were evenly

distributed throughout the bins the focus value for their study would have been F=0.167. If a 6-hour period had an F value greater than 0.5, the 6-hour period was considered to be 'focused' and the bin with the maximum number of counts was determined to be the focal bin. This method took into account differences in sample size, in that 6-hour periods with more dives (or more counts) required more focus to reach an F>0.5 (See Frost et al. 2001 for equation and details of calculations). Two juveniles were analyzed for focus in diving behavior using both methods to provide a comparison.

Statistical analyses

Statistical tests were conducted using SPSS 11.0. Differences between individuals grouped by season, sex and time-of-day were tested using MANOVA and matched pairs t-tests. Tests for multivariate normality were conducted using Mahalanobis distances (Tabachnick and Fidel 1996). Data were tested for normality and equality of variance using the Kolgomorov-Smirnov test for normality and Levene's test for equality of error variance. Data found to be non-normal were transformed using the appropriate transformation. Correlations were based on Pearson's correlations or Spearman's non-parametric correlations. Paired tests of dive duration, distance and haul-out duration as they related to maximum focus were tested using a matched pairs t-test. When data failed to pass tests for normality and could not be corrected by data transformation, non-parametric statistical tests were used.

Results

Time spent at depth

The calculated time spent at depth for the 17 juveniles in this study is shown in figure 5. Overall, juveniles spent a majority of their time near the surface either hauled-out or diving to depths less than 8 meters. Therefore, the analysis of dive behavior for this study accounts for approximately 17 % of the total time activity budget of these juvenile Steller sea lions. Most studies of pinniped diving behavior do not consider behavior at depths <4 m due to the resolution of dive instruments. The time spent hauled-out or above 8 m was not included in the model since juveniles were less likely to be foraging during this time, and the minimum depth for a dive was considered to be 6 m for this study.

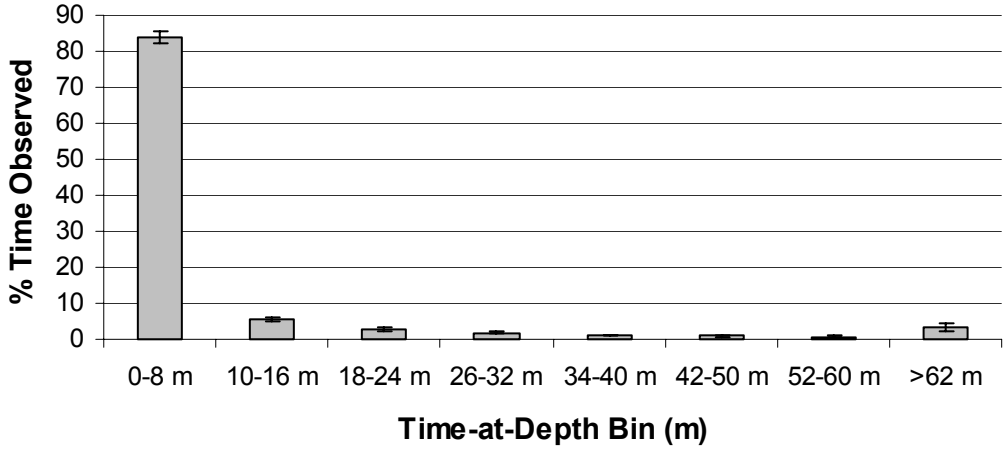


Fig. 5 The estimated mean percent time spent in various depth bins is shown for 17 juvenile Steller sea lions. Error bars represent SEM. The percent time shown in the 0-8 m bin includes all time hauled-out or resting at the surface.

Figure 6 shows the percent of time spent on land and at sea in various depth bins for 9 juveniles for which these data were available. These juveniles spent an average of 53% of their time on land and 28% of their time between depths of 0-4 meters. The remaining 19% of their time was spent at depths > 6 m. When examining time spent between the surface and 8 m, 32% of time was spent at sea between depths of 0 and 8 m for these 9 juveniles.

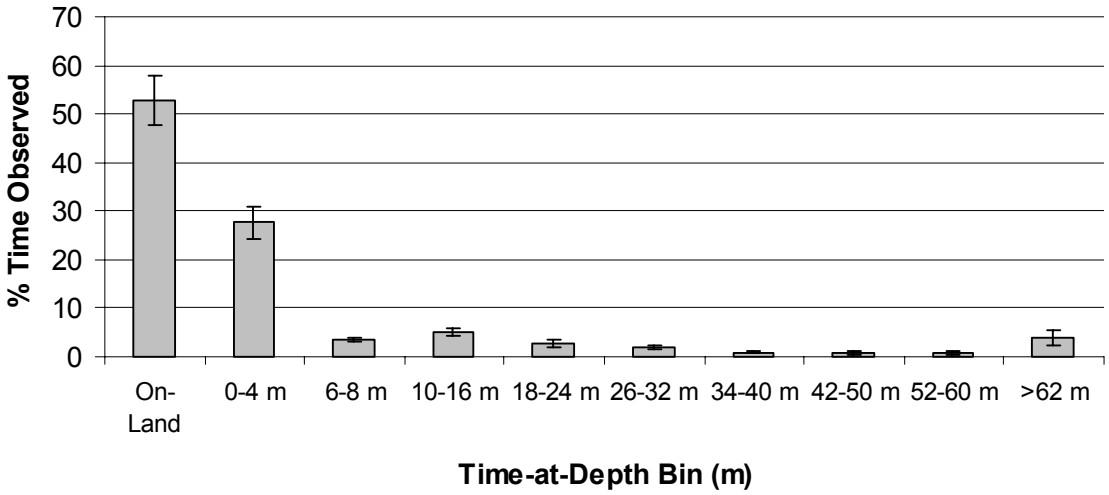


Fig. 6 The estimated mean percent time spent on land and at sea in various depth bins is shown for 9 juvenile Steller sea lions. Error bars represent the SEM. Data are taken from 5 males and 4 females released in varying seasons and locations.

Performance of the model

The focus, or observed time minus expected, (see Chapter I, page 2) is shown for various depth bins in Figure 7. Time spent in the shallowest bin analyzed for focus (10-16 m) was 28% greater than expected. Time spent in the deepest bin (62-162 m) was 19% less than expected. When the model was examined for variation from expected time spent in each bin, both the 10-16 m and 62-162 m bins were significantly different from expected (one sample t-tests with Bonferroni correction factor; t=6.413 and -4.465; $P < 0.001$ for both bins, df=16). Time spent in the 34-40 m and 42-50 m bins was also significantly less than expected (t=-8.43 and -8.188; $P<0.001$ for both bins, df=16), although these differences were not as large (mean differences -4% and -6%).

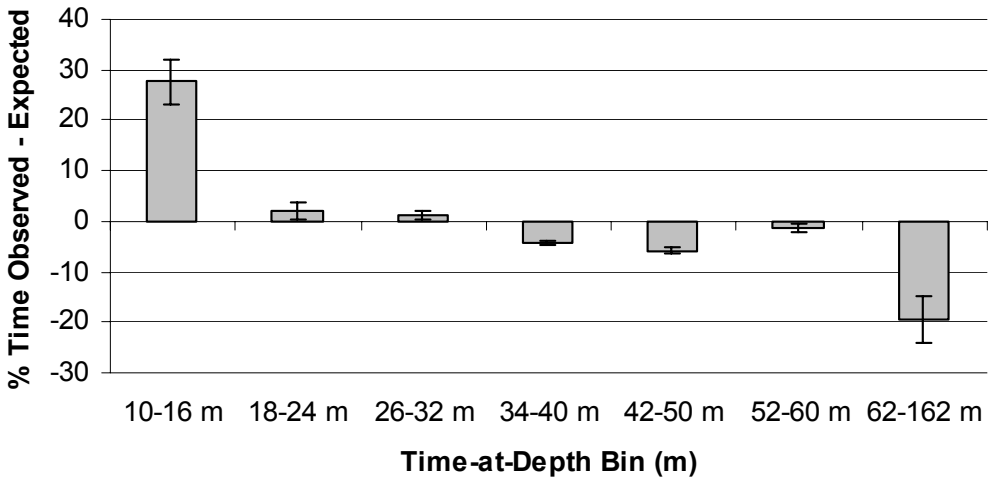


Fig. 7 Percent time observed minus expected for each time-at-depth bin is shown for 17 juvenile Steller sea lions released throughout the year in the Gulf of Alaska. Bars represent mean values with error bars showing the SEM. Expected values were derived from a model which assumed vertical travel to and from the surface at MCOT.

The observed proportion of dives by juveniles to depths of 62-162 m was 23%, which closely resembles the 21% of dives expected for these depths based on the assumptions of the model. Juveniles do not appear to be maximizing their bottom time for dives to depth. Based on the model, juveniles would be expected to spend 25% of dive time traveling and 75% of dive time in the 62-162 m bin if all dives were made to this bin in a 6-hour period. Five of the juveniles had 6-hour periods in which 100% of dives deeper than 9 m were to the deepest bin (62-162 m). These 6-hour periods did have an observed time spent traveling of 28% and time in the bin of 72%. Conversely, juveniles made 32% of dives to 10-16 m, which exceeded the expected percent of dives to these depths for the model of 23%. Although the expected percent of dives to 32-50 m was 20%, the actual percent of dives to these depths for juveniles was only 12%.

The longest dive duration used for the foraging trip model was 245 s (4.08 min). The calculated aerobic dive limit for juvenile Steller sea lions >1 yr in age ranged from 9.6 to 10.3 min (Loughlin et al. 2003; based on allometric equations from Schreer and Kovacs 1997). Five percent of dives exceeded 4.1 min in duration, with 17 dives greater than 9.0 min in duration. The model assumed that 12% of dives to depths greater than 9 m would have a duration of 4.1 min and that 18% of dives between 9 and 162 m would have a duration of 3.1 to 4.1 min. Of all dives, 9% had a duration between 3.1 to 4.1 min; however, this calculation includes dives to depths of 6-8 m, which constituted 31% of all dives. The remaining 68% of dives to depths > 9 m could not be sampled for duration.

TAD and other methods of describing dive behavior

The mean dive depth or duration for individuals is often calculated from SDR data by taking the midpoint of the range of the bin within which the maximum depth for each dive was located (See methods, Chapter II). For the 17 juveniles in this study, the calculated mean maximum depth of dives (with SEM error bars) is shown in Figure 8, overlaid with the percent focus in each bin based on TAD analysis.

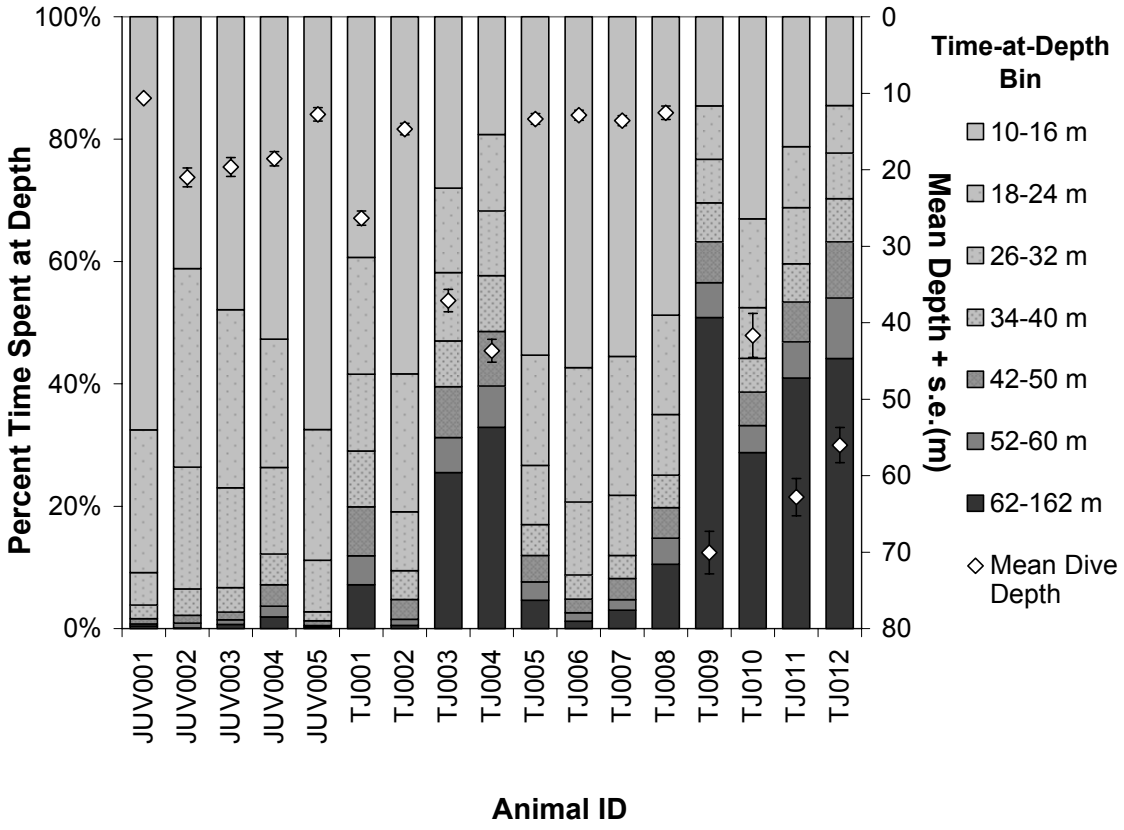


Fig. 8 Percent time spent in each time-at-depth bin for 17 juvenile Steller sea lions. Calculated mean dive depths with SEM bars for each individual are also pictured. Time-at-depth analysis is based only on 6-hr periods in which >30 min were spent below depths of 9 meters.

Calculated mean dive depths were often within the range of TAD bins in which the most time was spent for juveniles in this study (Fig. 8). Some exceptions are evident, particularly for individuals with a higher spread in proportion of time spent throughout the water column. For example, TJ003, TJ004, and TJ010 a male and two females released in winter, spent only 11%, 9% and 6% of their time below 9 m in the bin representing their mean maximum dive depth.

Comparison with other methods for determining focus

The dive behavior of two male juvenile Steller sea lions (JUV001, TJ011) released in summer and winter, was analyzed for focus using both the TAD method and depth bin count method (Frost et al. 2001) for a comparison of results (Fig. 9). Of the 29 6-hour dive depth histograms for JUV001 with >30 min spent at depths below 9 m, eight were considered to show focus (F>0.5) using the depth bin count method. Of these eight 6-hour periods, all were focused in the 10-16 m bin (Fig. 9a). Based on TAD analysis, an average of 76% more time than expected was spent in the 10-16 m bin for the eight 6-hour periods considered focused using the depth bin count method (mean ± se =75.60 ± 2.6 %, n=8). The average time spent in the 10-16 m bin for the remaining 21 6-hour periods analyzed was 47% greater than expected (mean ± se= 46.62 ± 3.00, n=21). For JUV001, focus in the 10-16 m bin is shown, with a reduction in focus in that bin when the juvenile increases focus at depth (Fig. 9a).

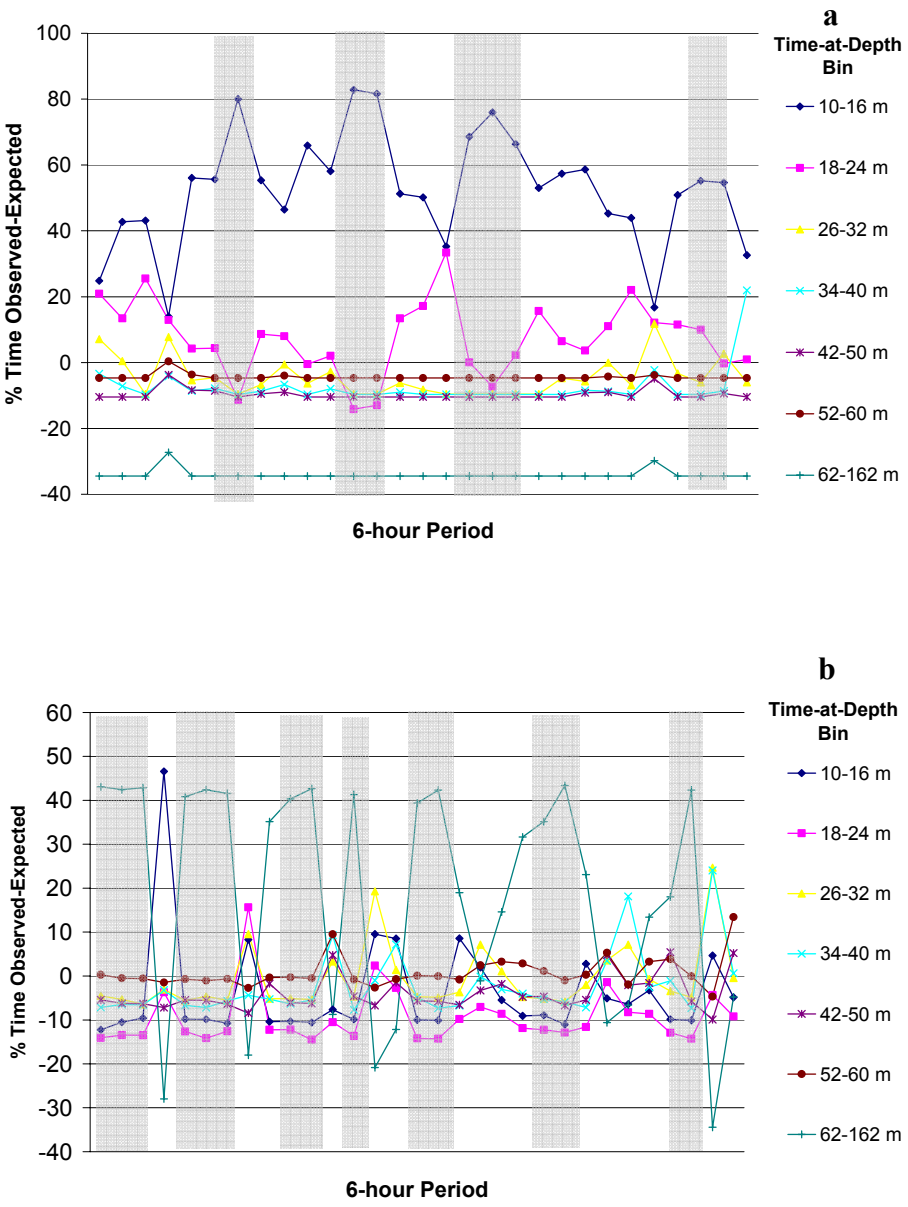


Fig. 9 The differences in percent time observed minus expected in 8 time-at-depth bins are shown for each 6-hour period for **(a)** juvenile JUV001 and **(b)** juvenile TJ011. Time periods which were found to be focused based on the depth bin count method (Frost et al. 2001) are shaded.

For juvenile TJ011, 15 out of 30 6-hour periods with >30 min spent below 9 m were considered to be 'focused' using the depth bin-count method. Of these, all were focused in the 62 -162 m bin (Fig. 9b). The percent time observed averaged 40% more than expected in the deepest bin for these 15 6-hour periods.

Variation in focus with mass and gender

Mass of the juvenile Steller sea lions ranged from 79 to 176 kg. There was a moderate positive correlation between mass and focus at depth (Table 4). Focus at depths of 42-50 m showed the highest correlation with mass.

Table 4 The results of a Pearson correlation between focus and mass are shown by TAD bin (the bin with the highest correlation is shown in bold).

Time-at-Depth Bin	**10-16 m**	**18-24 m**	**26-32 m**	**34-40 m**	**42-50 m**	**52-60 m**	**62-162 m**
Pearson Correlation	-.443	-.499	-.338	.606	**.669**	.564	.512
Sig. (2- tailed)	ns	.041	ns	.010	**.003**	.018	.036
N	17	17	17	17	**17**	17	17

To examine variation in focus between the sexes, the percent time observed minus expected in each time-at-depth bin was compared for male and female juvenile Steller sea lions (Fig. 10). The greatest focus for both females (n=9) and males (n=8) was in the 10-16 m bin (30 and 23 % more time spent than expected, respectively). The 62-162 m bin showed 24% less time than expected for females and 12% less time than expected for males. There was no significant difference in focus for any individual time-at-depth bin between the sexes (Kruskal Wallis, ns). Mean mass ± se of males (129 ± 8.5 kg) was slightly greater than females (119 ± 9.8 kg), although this difference was not significant (independent samples t-test; ns).

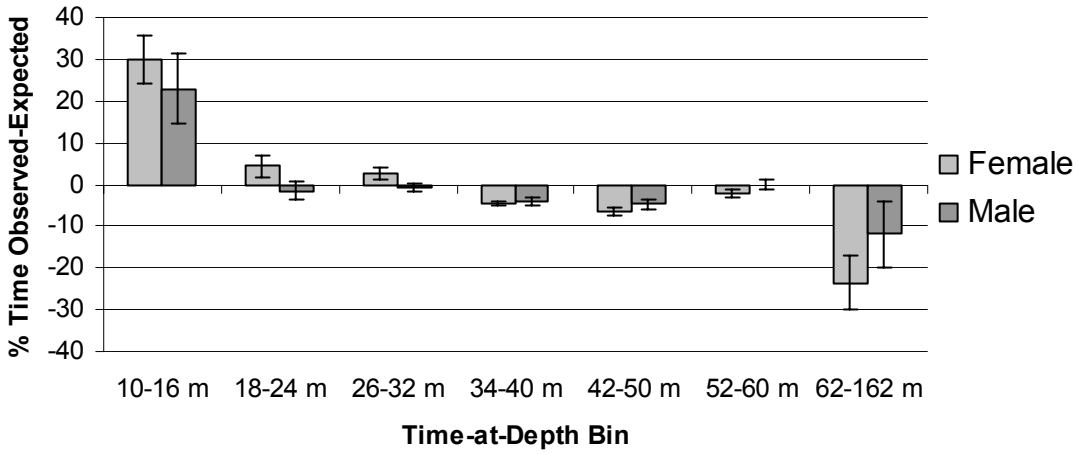


Fig.10 The percent time spent at depth (observed-expected) is shown for female and male juvenile Steller sea lions for each time-at-depth bin. Bars represent mean values with y-error bars showing SEM.

There was a significant difference in dive effort (# dives/hr) between females and males (t=-2.908, df= 9.035, $P<0.05$). Females performed a mean ± se of 10.33 ± 0.35 dives/hr and males 7.45 ± 0.93 dives/hr. Individuals did not show differences in number of dives per hour seasonally (independent samples t-test, ns) and dives per hour were not correlated with maximum degree of focus (Spearman correlation, ns).

Variation in focus with season and time of day

Sea lions monitored in both winter and summer showed the greatest focus in the 10-16 m bin. Juveniles spent 40% more time than expected in summer and 14% more time than expected in winter in the 10-16 m bin. Winter-released animals spent 6% less time and summer-released animals spent 32% less time than expected in the 62-162 m bin (Fig. 11). There were significant differences in time observed minus expected in 6 of the 7 time-at-depth bins (Table 5; Pillai's trace $P<0.005$) in summer versus winter.

Table 5 Differences in time observed minus expected, summer vs. winter, were significant for all time-at-depth bins except 26-32 m. Results were obtained using MANOVA.

Time-at-Depth bin	**10-16 m**	**18-24 m**	**26-32 m**	**34-40 m**	**42-50 m**	**52-60 m**	**62-162 m**
F	20.334	14.352	1.666	19.134	26.960	17.108	20.077
df	1	1	1	1	1	1	1
Sig.	$P<0.007$	$P<0.007$	ns	$P<0.007$	$P<0.007$	$P<0.007$	$P<0.007$

Winter-released juveniles showed significantly more focus than summer-released juveniles at depth. Summer-released juveniles were significantly more focused in the shallower time-at-depth bins (Fig. 11).

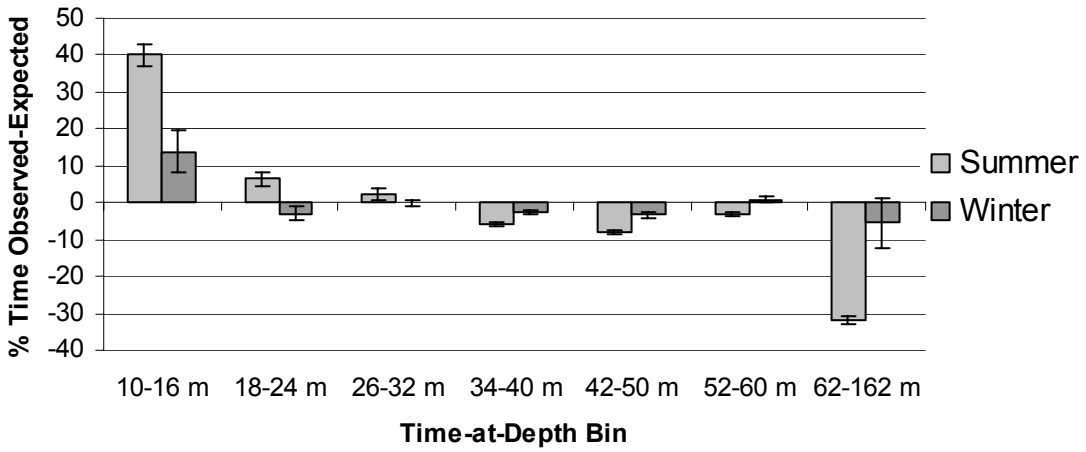


Fig. 11 Differences in focus with depth for juveniles in summer months (n=9; May-September) and juveniles in winter months (n=8; October – March), for each time-at-depth bin.

Juveniles monitored during summer months showed little variation in focus with time of day (Fig. 12). Seven of the 9 juveniles released in summer were more focused in the 10-16 m bin at night than at other times of day; however, focus in this bin did not differ significantly with time of day in summer (Wilcoxon signed ranks test, $P>0.05$).

The deepest time-at-depth bin (62-162 m) also did not show significant variation in focus with time of day in summer (Wilcoxon signed ranks test, P>0.05).

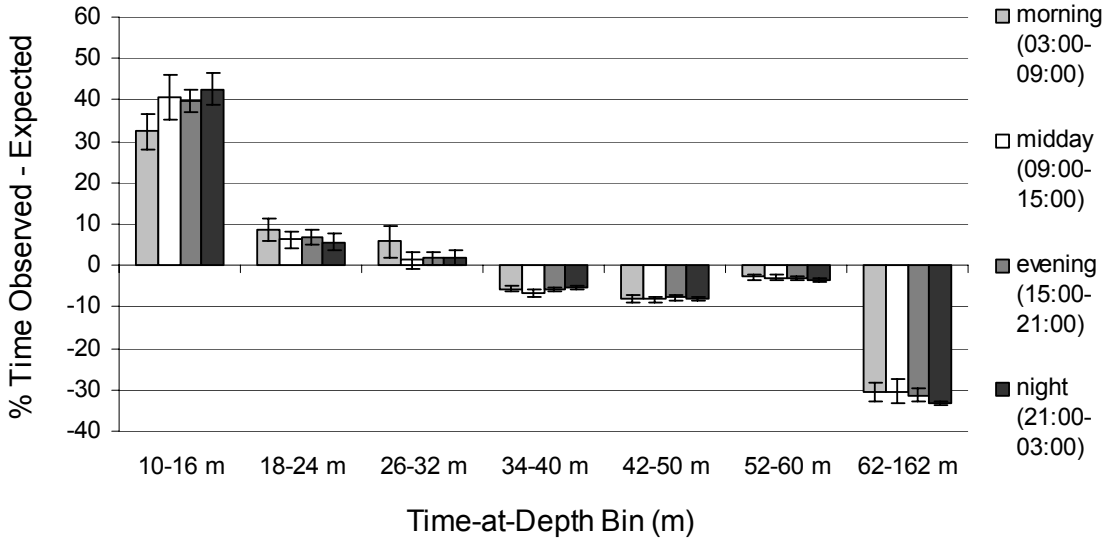


Fig. 12 The percent time observed minus expected in each time-at-depth bin for juveniles released in summer is compared by time of day. Bars represent mean values with y-error bars representing the SEM (n=9 sea lions).

As predicted, sea lions monitored in winter showed greater focus at depth during the few hours of daylight in the middle of the day in Alaska (Fig. 13). Focus at 62-162 m depth was significantly greater during midday than at other times of day for juveniles released in winter (Wilcoxon signed ranks test; Z=-2.240; P<0.05). There were no significant differences in focus at midday when compared with other times of day for the shallower time-at-depth bins in winter (Wilcoxon signed ranks test; P>0.05).

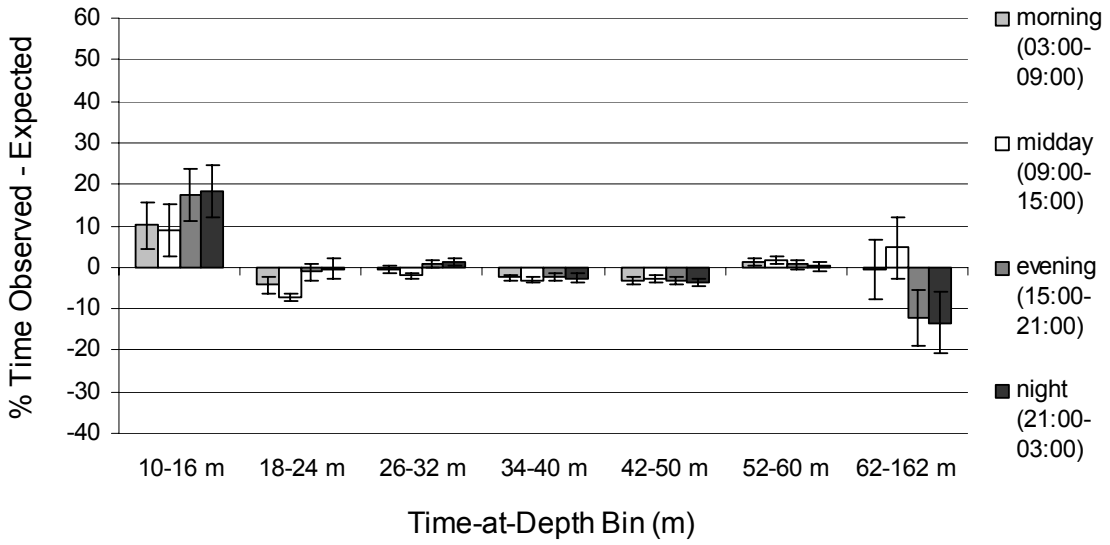
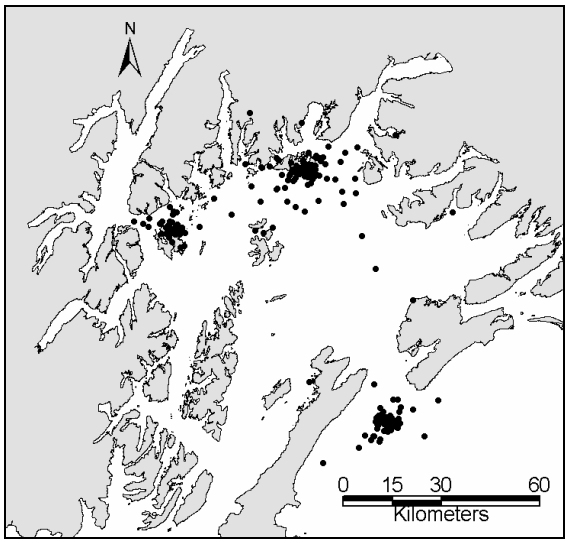


Fig. 13 Percent time observed minus expected for each time-at-depth bin for juveniles released in winter (n=8 sea lions). Bars represent mean values with y-error bars showing SEM.

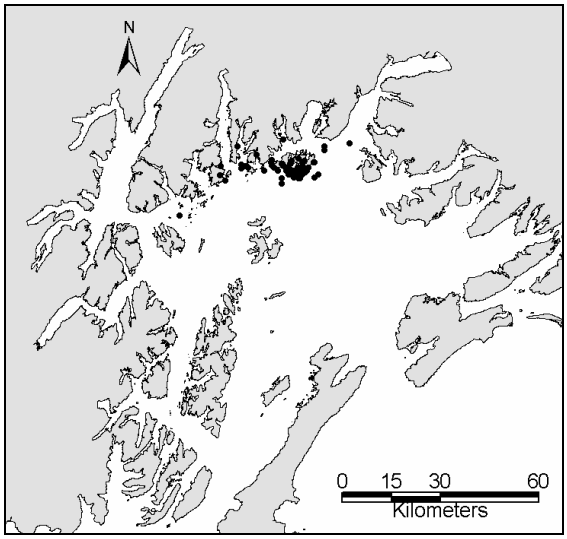
Focus and ranging behavior

Juveniles showed highly variable ranging patterns in summer and winter in the Gulf of Alaska (Figs. 14-17). Males and females released in Prince William Sound in summer showed typical ranging patterns for juvenile Steller sea lions (Figs. 14 and 15). Juveniles either remained near their capture location, or made transit trips to new haul-out locations in Prince William Sound. All juveniles released in summer remained within Prince William Sound during trips to sea.

a. JUV001



b. TJ008



c. JUV005

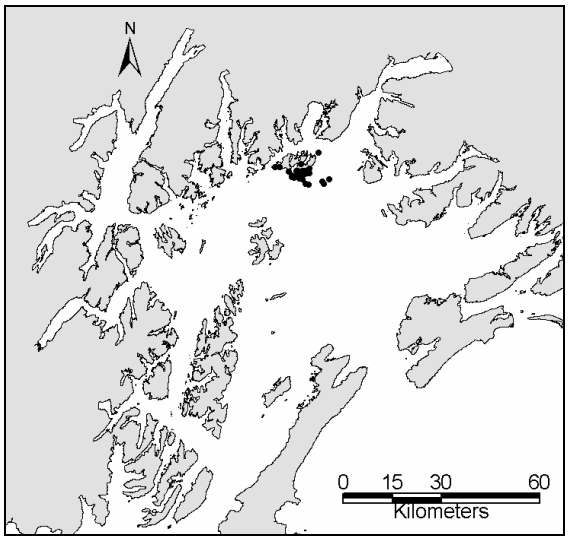


Fig. 14 Location data for three males released in summer (May-August) in 2004. Locations are shown in Prince William Sound with **(a)** JUV001 making transit trips between typical Steller sea lion haul-out locations in Prince William Sound and **(b) (c)** males JUV005 and TJ008 staying within the vicinity of Glacier Island (Please see Chapter II for details of typical haul-out locations for Steller sea lions in the Gulf of Alaska).

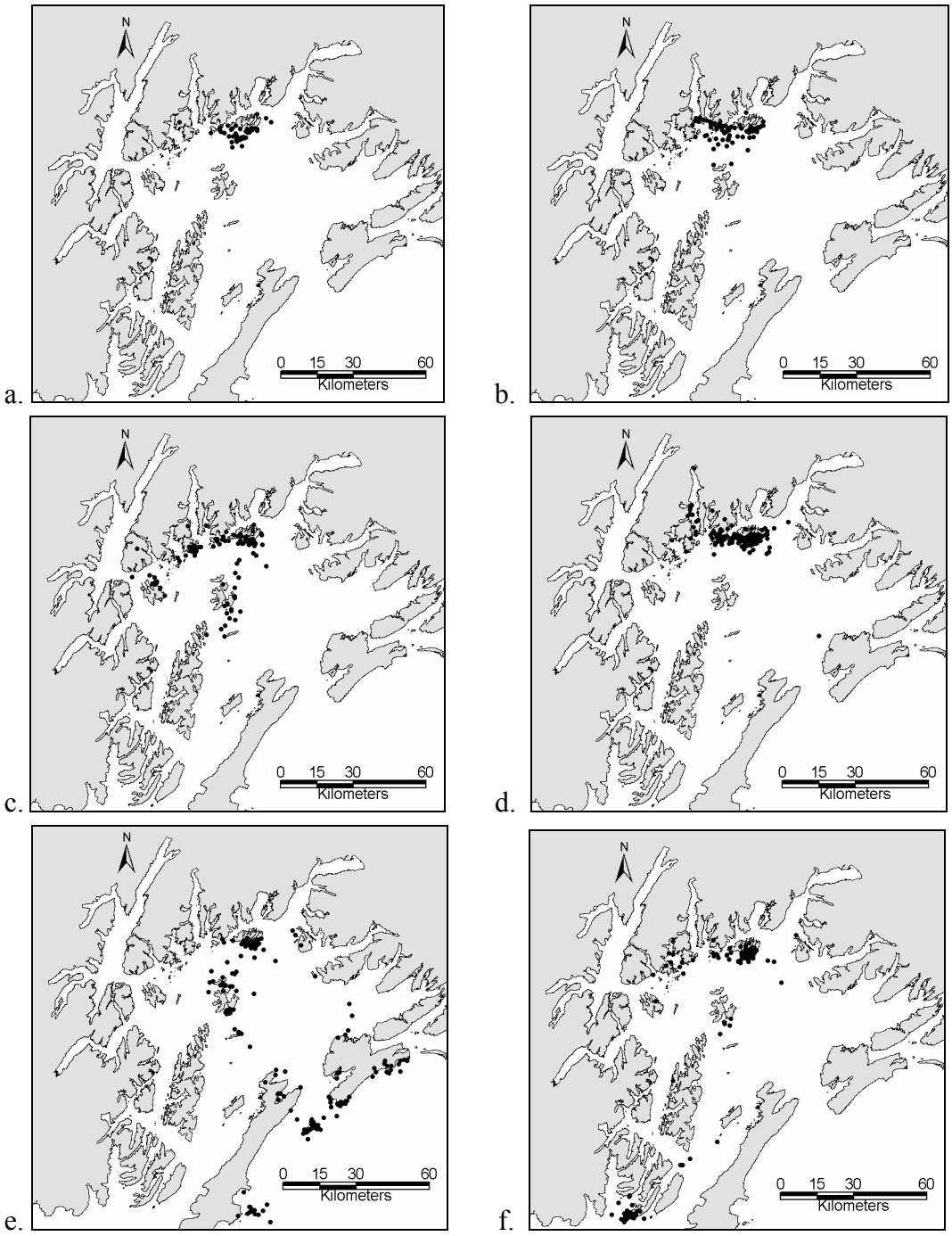
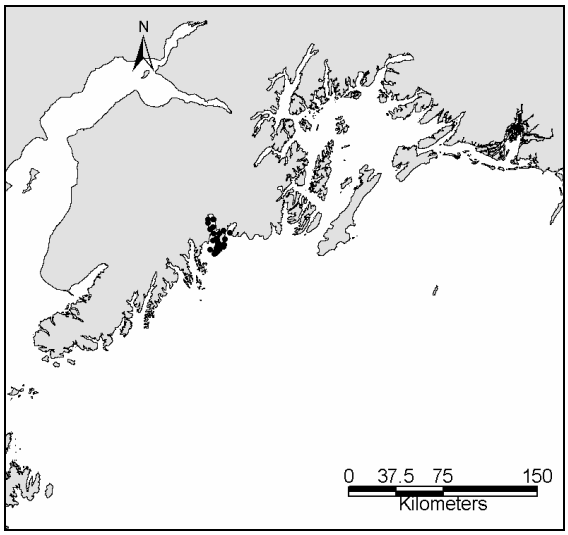
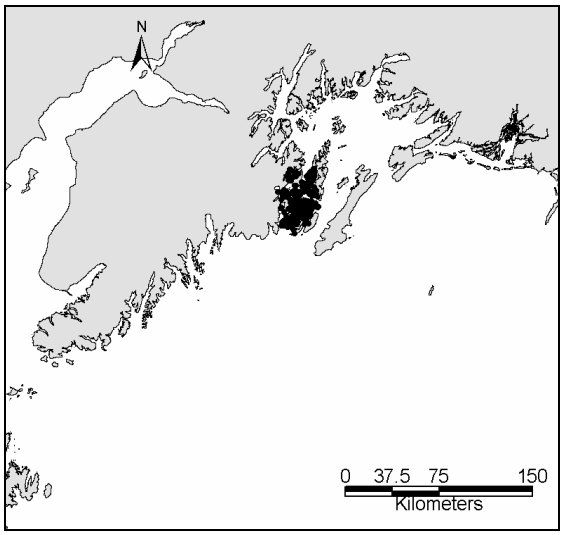


Fig. 15 Female juveniles released in summer in Prince William Sound including **(a)** JUV002 **(b)** JUV003 **(c)** JUV004 **(d)** T005 **(e)** TJ006 and **(f)** TJ007. TJ006 and TJ007 made typical transit trips to different haul-out locations.

a. TJ002



b. TJ004



c. TJ010

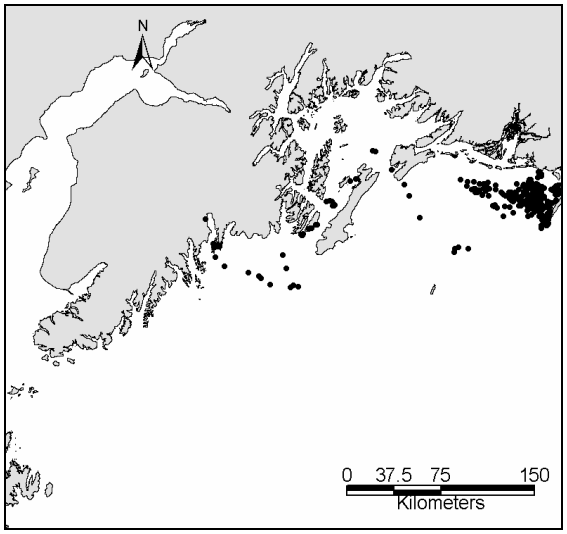


Fig. 16 The ranging behavior of three females released in winter in the Gulf of Alaska. High variability in individual ranging patterns are evident with **(a)** TJ002 remaining close to the capture location **(b)** TJ004 ranging in and around the lower portion of Prince William Sound and **c** TJ010 transiting to Cape St. Elias and then performing 'foraging-transit' trips continuously between Wingham Island and Cape St. Elias.

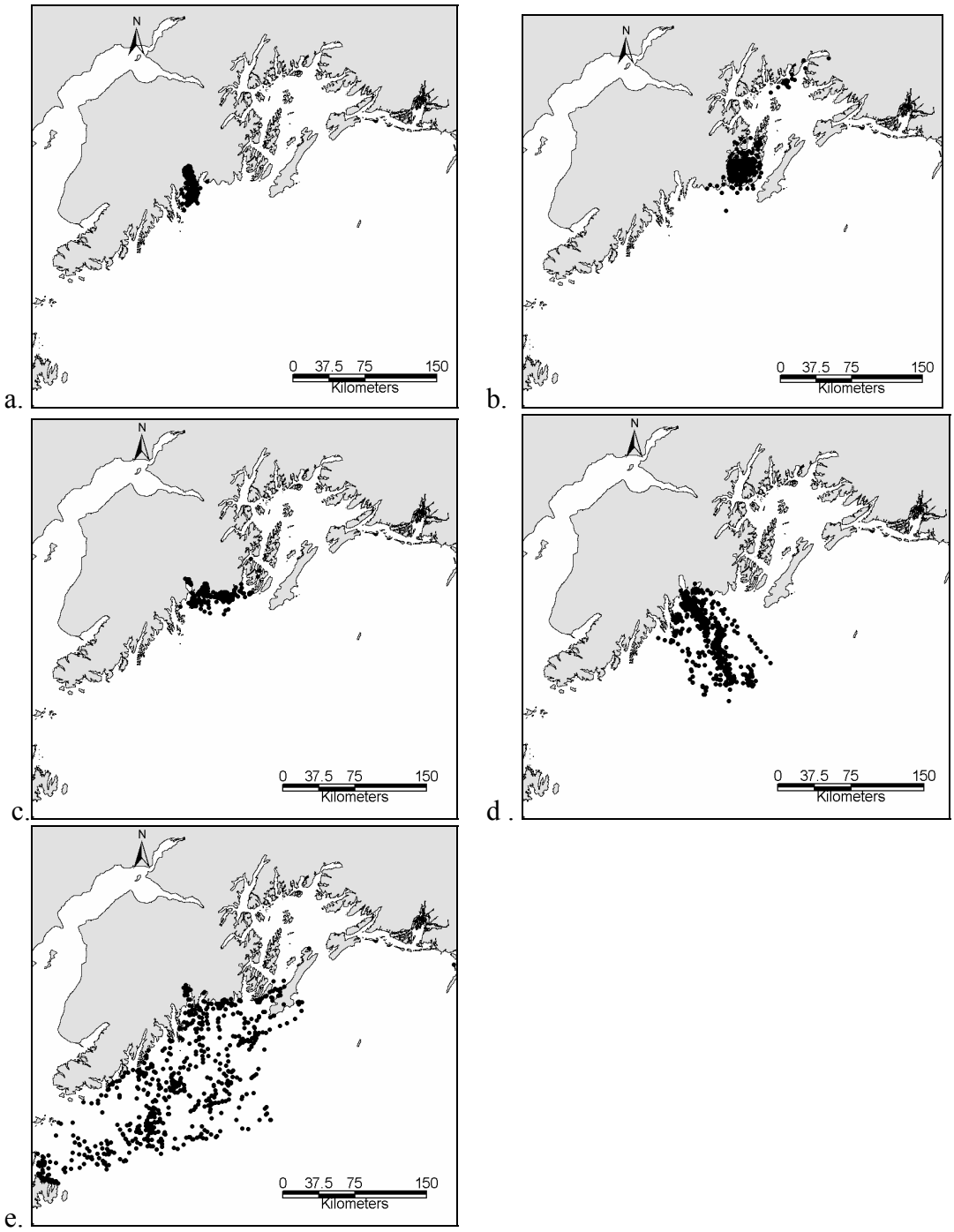


Fig. 17 Ranging of five juvenile males released in winter (October – April) 2003-2004 and 2004-2005 in the Gulf of Alaska. Variability in ranging behavior is evident with **a** JUV001 **(b)** JUV003 and **(c)** JUV012 remaining close to haul-out locations and juveniles **(d)** JUV009 and **(e)** JUV011 traveling to foraging locations offshore.

Males and females released in the Gulf of Alaska in winter showed extended ranging patterns with increased variability in haul-out locations and distances traveled while at sea (Figs. 16 and 17). Three types of trips to sea were defined based upon the ranging behavior of juveniles: foraging trips, transit-foraging trips, and transit trips (definitions derived from Loughlin et al. 2003). Foraging trips were round-trips to sea from the same haul-out location (Fig. 18). These round-trips had a mean ± se maximum distance traveled from the haul-out of 19.1 ± 3.29 km and a mean ± se duration of 20.8 ± 2.6 hours (n=16). Transit trips were trips directly from one haul-out to another with mean ± se transit trip distances and durations of 61.4 ± 11.4 km and 31.1 ± 1.1 hours (n=12; Fig.18c). A third type of trip, the "transit-foraging" trip, was also characterized for three juveniles released in winter (TJ010, TJ011 and TJ012). These trips included a substantial period of time spent at sea over the continental shelf before return to a different haul-out location (Fig.18 a,b). One juvenile, TJ010, made only this type of trip, consistently transiting between two haul-out locations with significant time spent at sea in different foraging locations (Fig.16c). Mean ± se transit-foraging trip distance and duration were 56.2 ± 7.9 and 52.6 ± 1.1 hours (n=3).

The mean ± se maximum round trip ranging distance was 19.1 ± 3.4 km (n=15; two of the juveniles never made round trips from the same haul-out). The mean ± se trip duration was 15.1 ± 2.5 hours. Mean ± se haul-out duration was 12.6 ± 0.7 hours. There was a moderate negative correlation between maximum focus and number of haul-outs used (r_s=-0.57; P<0.01). To review, "maximum focus" was defined as the percent time

observed minus expected in the time-at-depth bin with the greatest focus, or the greatest positive difference from expected behavior (see page 2, Chapter I; page 48, this chapter).

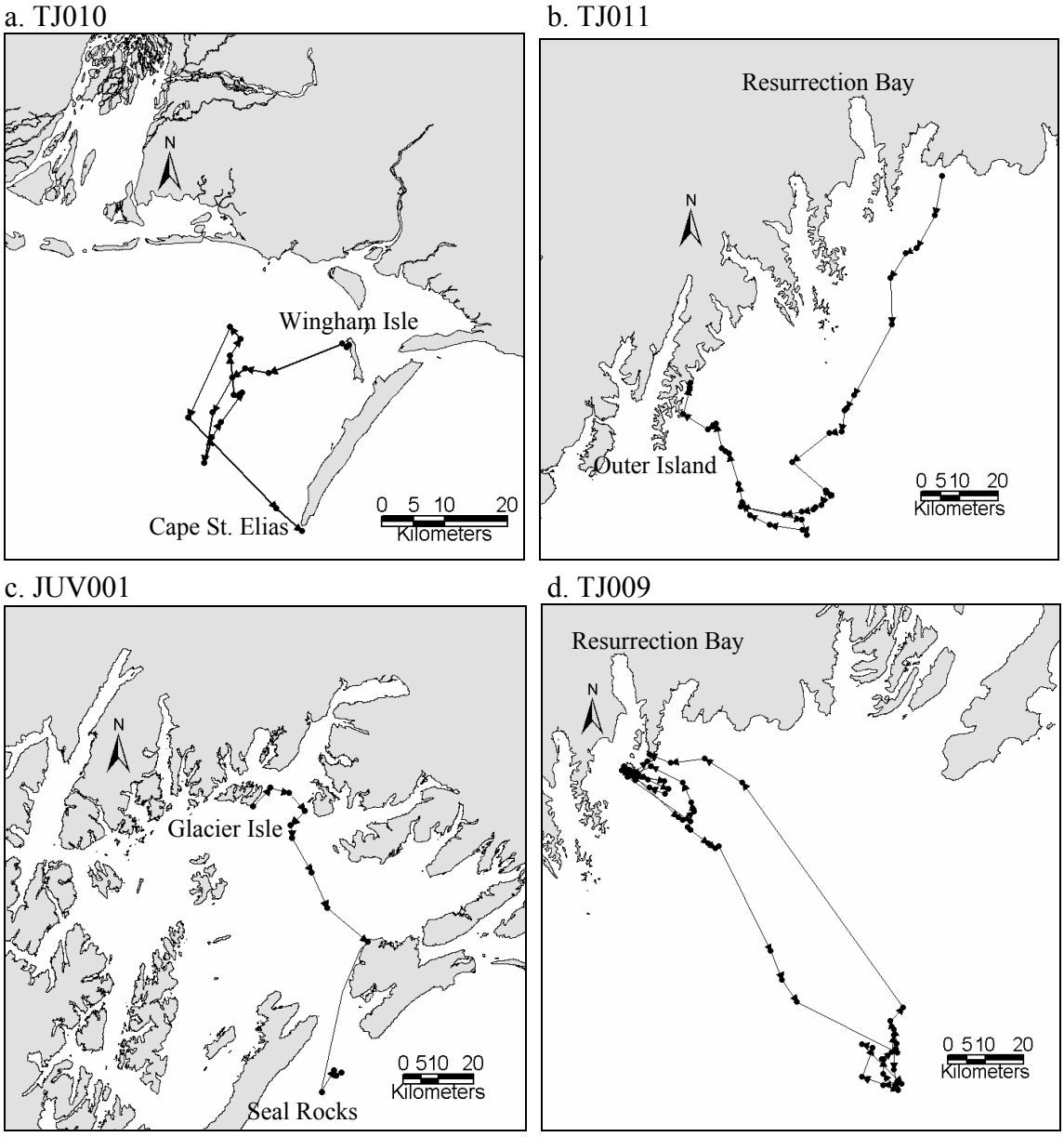


Fig. 18 Trips to sea defined as "transit foraging" trips for **(a)** a female and **(b)** a male released in winter. An example of **(c)** a 'transit trip' and **(d)** a short and long 'round-trip foraging trip' are also pictured for a male released in summer and a male released in winter.

There was a high negative correlation between mean trip duration and maximum focus (r_s=-0.85; P<0.01), with juveniles showing reduced focus having an increased mean trip duration. Juveniles showing reduced maximum focus were often winter-released animals which had more focus in the 62-162 m bin (Fig. 11). Greater focus at these depths showed a significant positive correlation with trip duration (r_s=0.70; P<0.01) as well as number of haul-outs used (r_s=0.62; P<0.01). There was no correlation between average haul-out duration or maximum round trip ranging distance and maximum focus.

When variation in trip duration and maximum focus was compared within individuals using a matched-pairs approach, short trips had a significantly greater maximum focus than long trips (matched pairs t-test, t=2.747, df=16, P<0.01,n=16). In addition, focus at depths of 10-16 m was also significantly greater for short trips when compared with long trips (Wilcoxon signed ranks test Z=-1.655, P<0.05; n=16). Juveniles traveled significantly further from haul-out locations during long duration trips (Wilcoxon signed ranks test Z=-3.124, P<0.001). Subsequent haul-out duration was not significantly different between short and long trips (Wilcoxon signed ranks test, ns).

Eleven of the juveniles made both round-trips to sea and transit trips to new haul-out locations. The number of haul-outs used ranged from 14 to 2. The mean time between transit trips was 9.2 days. The shortest time between transit trips was 5 days (TJ012). There was no significant difference in focus just prior to transit trips for any of the 7 TAD bins (Wilcoxon signed rank test, P>0.05).

Discussion

Focusing on time spent at depth

Analysis of time spent at depth for pinnipeds allows for new evaluations of foraging behavior, including focus in time spent at varying depths. Most examinations of pinniped dive behavior to date have used variables such as mean maximum dive depth and duration to quantify foraging behavior of individuals (Walker and Boveng 1995; Frost et al. 2001; Loughlin et al. 2003; Simpkins et al. 2005). Time spent at varying depths has been examined for data obtained from individual dives recorded by time-depth recorders; however, these relationships have been examined in the context of particular 'dive types' rather than overall time spent at depth (Lesage et al. 1999; Le Boeuf et al. 2000). Although SDR data are necessarily binned, reducing the detail of the data available for analysis, the collection of vertical location in the water column at relatively good resolution (every 10 seconds) can indicate how juveniles are focusing their foraging efforts.

Many studies of pinniped diving behavior do not consider behavior at depths <4 m as dive behavior due to the resolution of instruments (Boyd et al. 1997; Lesage et al. 1999; Frost et al. 2001; Loughlin et al. 2003). The percent time spent between 0 and 4 meters is likely to include time spent resting at or near the surface, traveling, and a compilation of the surface durations of individual dives. The 32% of time spent at sea between the surface and 8 m noted for 9 juveniles in this study may also include

foraging time. Foraging behavior has been noted in depths of <10 m for Steller sea lions during summer months in Alaska (W. Schrader, personal observation). Foraging behavior has also been described for other pinnipeds during dives to less than 4 m in similar habitats (Lesage et al. 1999).

The analysis of focus in diving behavior for juvenile Steller sea lions in this study examines only a portion of the overall time-activity budget of individuals. Examination of dive behavior is necessarily important for diving mammals, particularly otariid seals, which are known to spend time near the surface either resting or traveling, and time at depth foraging (Boyd et al. 1994) rather than performing other activities at depth as has been reported for phocid seals (Le Boeuf et al. 2000). The time that an otariid seal spends beneath the surface, although a small proportion of overall time spent, may be crucial to individuals as it is likely to make up the majority of time spent at the greatest energetic expense and at the limits of habitat availability. The edges of an individual's range may be quite important foraging areas, possibly even more important, than the centers of their ranges. This is particularly true for juvenile diving mammals which are constantly expanding their diving and ranging capability as they develop.

Modeling time-at-depth with respect to focus

The model for time-at-depth focus presented in this chapter was built with two related assumptions: Individuals were expected to 1) maximize their time at the bottom of each dive and 2) travel vertically to and from the surface (in order to accomplish this), at the minimum cost of transport for juvenile Steller sea lions. Although it has been assumed that the maximum depth reached in any dive is the focal depth for that dive (Frost et al. 2001), this may not be the case for juvenile Steller sea lions. Juveniles made more than the expected number of dives to depth, but did not spend the expected percentage of time at depth. Therefore, the use of the maximum depth of individual dives as the "foraging depth" or "focal depth" for otariid seals may not accurately reflect the importance of other portions of the water column visited by individuals during a dive.

The distribution of percent time spent at depth for 5 juveniles which had 6-hour periods which were entirely focused in the deepest bin, implies that when juveniles are making focused dives to depth (i.e., 100% of dives are to the same depth bin in a 6-hour period) they follow the general assumptions of the model with regard to vertical dive angle, travel at the MCOT and maximizing time spent at the bottom of dives. However, when the maximum depth of individual dives is distributed throughout the water column in a 6-hour period, angle and speed of individual dives also appears to vary. If higher distribution of maximum depth of dives implies increased searching behavior for a 6-hour period, variable dive angle and travel speed may also indicate increased searching

behavior. Searching dives could very well be less individually focused than feeding dives in which juveniles are actively ingesting a prey patch that has already been located.

Juveniles may spend more time traveling through upper portions of the water column during individual dives, either by changing orientation or speed, or spending less time than expected at depth due to other constraints on dive duration. The greater focus in shallow bins may be due to both more time spent traveling through these bins than expected and increased diving to these depths for juveniles in this study. The reduced number of dives made to depths between 32-40 m when compared with expected values based on the model may explain the reduced focus in these bins when compared with expected values for these depths.

Allometric equations for aerobic dive limit assume conservation of energy during diving either by traveling at the MCOT for juveniles to and from the focal depth of a dive or using other strategies to minimize energetic expense during diving (Schreer and Kovacs 1997; Williams 2001). Searching for and consuming prey at depth may require juveniles to expend more energy so that dive duration is cut short. For juveniles diving to depth, then, the benefits must far outweigh the costs.

Methods of calculating focus

The dive depth bin method for examining focus (Frost et al. 2001) was applied to harbor seal dive records obtained in Prince William Sound using similar instruments. The results of the study showed that 6-hour periods were focused in the maximum depth of dives in particular depth bins. Variability in focal depth was described as related primarily to habitat variability (Frost et al. 2001), although degree of focus using this measure also varied with sex and time of day. The method described by Frost et al. (2001) appears to be conservative in its estimation of focus in that only 6-hour periods with relatively high focus (76% greater than expected for JUV001 using the TAD method) are considered to be 'focused' using the dive count method. The TAD method considers all 6-hour periods and examines focus in each bin.

Based on the behavior of juvenile Steller sea lions in this study, using the maximum depth of individual dives to quantify degree of focus may not truly reflect water column use by juveniles. In addition, correction for availability of different depths to individuals with distance from the surface, whether based on development of a null model or a model based on the typical behavior of the species in question, may improve the evaluation of focus in diving behavior.

Differences in focus with mass and gender

The relationship between mass and focus in deeper bins indicates that larger juveniles are capitalizing on prey at depths that may be physiologically unavailable to smaller juveniles. As juvenile pinnipeds develop in both motor capacity and blood oxygen stores, they often increase the depth and duration of dives (Burns et al. 1997; Horning and Trillmich 1997). Prey sources at depth may be more physiologically available to larger juveniles, which would affect the expected time spent for larger juveniles at depth. There were no differences in focus for any of the depth bins when examined by sex, and males were not larger than females in this study. The relative blood oxygen stores between male and female juveniles were not measured, but behavior does not indicate that males had an advantage over females in accessibility of prey at depth.

The increased dive effort for juvenile females in this study is consistent with differences in dive effort between males and females reported for adult female grey seals (Beck et al. 2003). Although females were not significantly more focused than males in any time at depth bin, they made more dives per hour to attain the same focus in the different time-at-depth bins. The increased focus in diving behavior reported for female grey seals (Beck et al. 2003) and female harbor seals (Frost et al. 2001) may not be evident until differences in mass and reproductive effort begin to affect the way in which females interact with depth when compared with males.

Seasonal and diel patterns in focus

Juvenile Steller sea lions appear to change the focus of their diving efforts, spending more time at depth in winter than in summer, and greater focus at shallower depths in summer than winter. This difference in distribution of time spent at depth is likely a result of differences in locations of prey resources seasonally in the Gulf of Alaska. The observed seasonal difference in time-at-depth focus follows that predicted if focus is an indicator of prey accessibility, based on available information regarding seasonal variation in prey distribution. This provides indirect evidence that focus in water column use is indeed linked to prey accessibility for juvenile Steller sea lions.

There was no significant diel variation in focus during summer for juveniles in this study. Steller sea lion prey species in the Gulf of Alaska, although they are more accessible at night from the surface, have also been characterized as more dispersed at night (Fadely et al. 2003). This increased dispersion of prey items may counteract the increased accessibility of prey from the surface, resulting in no significant increase in focus of foraging efforts at night in summer. Other studies of juvenile Steller sea lions have found increased diving effort at night with a resulting increase in time spent at depths greater than 6 m. However, the time juveniles spend foraging at night does not appear to be more focused than time spent at depth for other times of day. An analysis of focus with time of day can elucidate smaller scale interactions between juvenile otariids and their prey. In this case, increased foraging effort does not necessarily imply increased prey accessibility to individuals. In fact, juveniles may be managing the costs

of foraging at depth during the day on more aggregated prey patches versus foraging at night on more highly dispersed prey which are closer to the surface. In this case, prey accessibility may be relatively constant for both foraging strategies.

Reduced diel vertical prey migrations in winter, with a corresponding increase in prey aggregations at depth, appear to affect the foraging strategy of juveniles. The best strategy for juveniles foraging in winter may be to capitalize on available light sources, and forage during the limited daylight hours on aggregated prey species at depth. Juvenile Steller sea lions in this study appear to be using this foraging strategy in winter, with an increase in focus, and therefore prey accessibility, during midday, rather than at other times of day.

Optimal foraging trip predictions and focus

The significant negative correlation between maximum focus and overall trip duration implies that focus may be a good indicator for prey accessibility. Foraging trip duration has been described as the best indicator of prey accessibility to lactating female otariids (Gentry and Kooyman 1986; Walker and Boveng 1995; Boyd et al. 1997). Trip duration was also correlated with focus at depth. For juveniles focused at depth, an increase in trip duration may be another indication of reduced prey accessibility. The moderate negative correlation between maximum focus and number of haul-outs used by juvenile

Steller sea lions may further substantiate focus as an indicator of prey accessibility, as focus decreases with an increase in horizontal foraging range.

The matched-pairs approach to examining maximum focus and foraging trip parameters provided the best comparison of changes in maximum focus with changes in ranging behavior. Individuals showed greater maximum focus for short trips when compared with long trips. This result supports the hypothesis that focus in the water column may be a good indicator of prey accessibility to individuals. Analysis of focus and how it relates to foraging trip parameters provides a new approach to the use of dive behavior to indicate prey accessibility.

Analysis of focus would be more detailed and reflective of changes in focus at depth if records of individual dives for juvenile Steller sea lions were applied to this method. More detailed data relating to both the diving behavior of individuals, as well as a real-time characterization of their individual prey fields, would further substantiate whether focus in diving behavior indicates prey accessibility to individuals.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Juvenile Steller sea lions are as individually varied in their daily habits, including ranging and hauling-out patterns and diving behavior, as most any other juvenile pinniped. However, a few central tendencies in juvenile (>1 yr) Steller sea lion behavior can be gleaned from the remote monitoring of individuals using SDRs. Juveniles range to distances and depths that are comparable with adult Steller sea lions. They are found at typical haul-out locations for Steller sea lions throughout the year, and, according to this study, can certainly travel distances that exceed the geographic separation of eastern and western U.S. populations of Steller sea lions, although none of the juveniles from this study were found to do so.

Seasonal variation in dive depth and duration was consistent using two different methods of characterizing dive behavior based on data collected by SDRs. The mean maximum depth and duration of individual dives increased from summer to winter months for juvenile Steller sea lions (Chapter II). Time-at-depth data also indicated an increase in time spent closer to the surface in summer and at depth in winter months (Chapter III). The mean maximum depth of dives reflected the greatest use of the water column at depths ranging from 16 - 34 m (Chapter II) for juveniles. Analysis of time-at-depth data revealed the greatest time was spent in depths of 0-8 m when the animals were at sea, with additional peaks in water-column use at 10-16 m, and > 62 m in winter months (Chapter III).

Ranging behavior of juvenile Steller sea lions observed in this study was typical of that reported in other studies. The offshore foraging trips of juvenile males released in winter in the Gulf of Alaska were particularly impressive, as well as the long-range transit trips of >300 km to new haul-out locations made by both males and females. The ranging behavior of juveniles in this study implied high individual variability in foraging strategies. Juveniles released in winter, although more likely to range further during individual foraging trips, had consistent individual patterns in foraging behavior. For example, juveniles that traveled offshore during foraging trips tended to continue to do so when compared with juveniles that remained close to land during foraging, regardless of season or length of time they were monitored. This individual 'habit' in foraging behavior would be interesting to examine further to see how these individual patterns in foraging behavior develop and if they are maintained into and throughout adulthood. Unfortunately, the number of juveniles monitored in this study and the length of observation per individual precluded the examination of individual variability in foraging behavior with season and habitat type.

Juvenile Steller sea lions do not appear to accrue any significant adverse effects from periods of temporary confinement for research purposes. The post-release diving and ranging ability of juvenile Steller sea lions which experienced up to three months of captivity seemed unimpaired. Lack of significant differences in duration of dives for temporarily captive juveniles and the long (>4.2 min) dive durations performed by all 12 temporarily captive juveniles within the first few weeks after release were the best indication that temporary captivity did not reduce dive performance of juveniles. The

result of this temporary confinement and release of healthy individuals should further inform the numerous rehabilitation and relocation efforts which are on-going for marine mammals throughout the world. Of course, any long-term effects of temporary captivity on survival and reproduction could not be monitored during this study. Re-sighting of branded individuals, as well as the monitoring of newly released individuals which receive Life-History Transmitter (LHX) implants (Horning and Hill 2005) will provide a longer term indication of the effects of temporary captivity on behavior and survival into adulthood.

The detailed analysis of time spent at depth for juvenile Steller sea lions in this study allowed for a unique examination of foraging behavior as it relates to water column use and foraging trip parameters. This new approach, based on time spent at depth by juveniles and how it varied from expected values, was useful for examining changes in focus in the water column with season, time of day, and ranging behavior. The 'binned' nature of SDR data does not allow for a detailed examination of individual dives; however, the vertical distribution of time spent by juveniles in the water column with 10 s resolution, provided a good indication of how juveniles focus their foraging efforts per 6-hour period.

The analysis of focus in diving behavior showed individual variability in dive behavior based on focus in the water column. When juveniles were focused only in the deepest time-at-depth bin (>62 m), they appeared to travel vertically through the water column and maximize bottom time of dives. Juveniles with an increased range in time spent at depth also showed variability in number of dives to different bins with an

implied increased variability in dive angle of individual dives. The model used to assess variability in focus for time-at-depth parameters was based on data obtained from juvenile Steller sea lions in other studies. Individuals were also expected to 1) maximize their time at the bottom of each dive and 2) travel vertically to and from the surface at rates consistent with the minimum cost of transport for juvenile Steller sea lions. The overall departure from the model that juveniles exhibited implies that the maximum depth reached in any dive is not necessarily the 'focal depth' for that dive. Based on these observed differences, a greater distribution in time spent at depth per 6-hour period implied increased variability in dive angle and travel speed, which may be a result of increased searching behavior.

Seasonal and diel variation in focus indicates that water-column use can be linked to prey accessibility for juvenile Steller sea lions. Differences in focus are likely a result of seasonal differences in locations of prey sources and diel variation in locatability of prey sources in the Gulf of Alaska. Analysis of focus in time-at-depth data when compared with other times of day can elucidate smaller scale interactions between juvenile otariids and their prey. Increased foraging effort, such as number of dives per hour, did not necessarily imply increased prey accessibility to individuals. Juveniles appeared to be managing the costs of foraging at depth during the day on more aggregated prey patches with foraging at night on more highly dispersed prey that are closer to the surface.

The significant negative correlation between maximum focus and overall trip duration provided the best indication that focus may be related to prey accessibility.

Foraging trip duration has been described as the best indicator of prey accessibility to lactating female otariids (Gentry and Kooyman 1986; Walker and Boveng 1995; Boyd et al. 1997). The matched-pairs approach further substantiated the relationship between maximum-focus and foraging-trip parameters. The decreased maximum focus for juveniles conducting long versus short foraging trips supported the overall hypothesis that focus in the water column may be a good indicator of prey accessibility to individuals. Analysis of vertical focus in the water column for pinnipeds would be more detailed if records of individual dives were applied to this method, such as data obtained from time-depth-recorders. To confirm if pinnipeds which are most focused in their dive efforts experience higher prey accessibility, individual prey fields of foraging pinnipeds should be examined in real time with quantification of prey patch quality, rate of prey patch encounters, prey ingestion rates and other diving and ranging parameters for individuals. As instruments and techniques for characterizing the diving and ranging behavior of pinnipeds develop, some of these questions may begin to be answered. In the meantime, it appears that focus in water column use can be related to prey accessibility for juvenile otariid seals. Variation in focus in foraging efforts can be used as an additional response to examine changes in prey accessibility to individual foraging seals in the fluid environments in which they live.

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